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CONTENTS

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THE LIFE OF FLATHEAD LAKE, MONTANA

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* Resigned 1934.

CONTENTS

THE LIFE OF FLATHEAD LAKE, MONTANA

INTRODUCTION

In the summer of 1928 the Montana State Fish and Game Commission undertook an investigation of Flathead Lake to determine means of increasing its production of food and game fish, especially the eastern, or Lake Superior whitefish, *Clupea clupeaformis*, several plantings of which had produced only meagre results. The work was placed in charge of the biological staff of the University of Montana at Missoula, assisted by the departments of Physics, Chemistry and Geology. Active work was prosecuted from 1928 to 1932, the results of which are presented in the following paper.

I wish to express here our indebtedness to the Commission for their interest and financial assistance, to former Chancellor M. A. Brannon, President C. H. Clapp and Dr. M. J. Elrod for their cordial support of the project, while to my colleagues, Drs. G. D. Shallenberger and J. W. Howard, I am obligated for many of the data on the physics and chemistry of the lake. The U. S. Bureau of Fisheries aided us materially by the loan of equipment. For the botanical data I am indebted to my former colleague, Dr. J. E. Kirkwood, whose death in 1928 was a serious blow to our work; and to Dr. C. W. Waters, who succeeded Dr. Kirkwood in 1929.

For assistance in identification of material I am indebted to the following: Prof. Bert Cunningham, Protozoa; Dr. G. B. Twitchell, sponges and Bryozoa; Dr. Libbie H. Hyman, planarians; Mr. F. J. Meyers, rotifers; Mr. Gerald Thorne, nematodes; the late Dr. C. Dwight Marsh, copepods; Prof. Paul Welch, annelids; Dr. J. P. Moore, leeches; Dr. R. E. Coker, canthocamptids; Dr. E. A. Birge, cladocerans; Dr. W. L. Tressler, ostracods; Dr. J. G. Needham, Dr. O. A. Johannsen, Prof. H. B. Hungerford and the staff of the U. S. Nat. Museum, insects; Dr. Ruth Marshall, water mites; Dr. Junius Henderson and the late Dr. V. Sterki, molluscs; and Prof. C. J. Elmore, diatoms.

The plancton counts were made by Miss Elizabeth Barto, and most of the graphs by Mr. Russell Watson.

PREVIOUS WORK

Many of the European lakes have been thoroughly studied hitherto and there are several studies on those of North America, but no thorough work has yet been done on any of the mountain lakes in this country, although preliminary investigations have been made on several.

Especial interest attaches to a study of Flathead Lake by the previous observations of Forbes (1893), rendering some comparison possible between present and past conditions; and more especially, by the probable construction of a dam below the outlet of the lake, which will, if completed, raise its

level by several feet and undoubtedly alter materially the present environment.

What are the present physical, chemical and biological conditions in Flathead Lake are questions which this paper will attempt to answer, as a basis of comparison for studies which may be made in the future when present conditions have been changed.

Stations

In the study of the lake, ten stations, which are shown on the accompanying map, were selected to represent, as nearly as possible, all of the different environments in the lake. Stations 2, 3 and 8 were in water averaging less than 3 m. in depth, while the others were at varying depths, down to 90 m. (No. 1). The environment at No. 4, just inside the mouth of the Flathead River, is very different from that in the open lake. The temperature averages about 3°C lower than at corresponding levels in the adjoining lake and the river carries a considerable load of sand and silt, which is being deposited in an extensive sand bar at its mouth.

Station 5 in a chain of islands cutting off Polson Bay from the main lake, is in a passage 100 m. wide and about 15 m. deep at low water, through which flows a large part of the water in the lake. This is the only point at which a current, due solely to the flow of the lake, has been detected.[1]

Observations were made at each station approximately twice a month during July, August and September 1928, and once a month from June to September in 1929. Additional collections were made at some of these stations at irregular intervals. At one of the stations (No. 1), selected to represent as nearly as possible the lake as a whole, observations were made at 6 to 14 day intervals from July 5 to November 3, 1928. In 1929 one series of observations was made in February, while from April 16 they were made bi-weekly or oftener until November 28, with exception of the intervals from July 12 to 31, August 9 to 30 and November 9 to 28. Thereafter one series was made on December 19 and 20 and one on February 3, 1930, when the plancton collections were ended.

In September 1930, and March to September 1932 several series of bottom samples for quantitative study were taken in Yellow Bay and the adjacent lake to determine depth distribution of the benthos. Besides these collections a large number of samples for qualitative study were made at many places in the lake, representing all possible habitats therein, and a few samples for quantitative study were made at points other than those enumerated above.

Topography and Geology[2]

Flathead Lake is 43 km. long and 24 km. wide. Its principal tributary is Flathead River which is formed by the union of three large forks about 50 km.

[1] See page 107.

[2] The data on geology and topography of Flathead Lake have been taken from a ms. report by President C. H. Clapp.

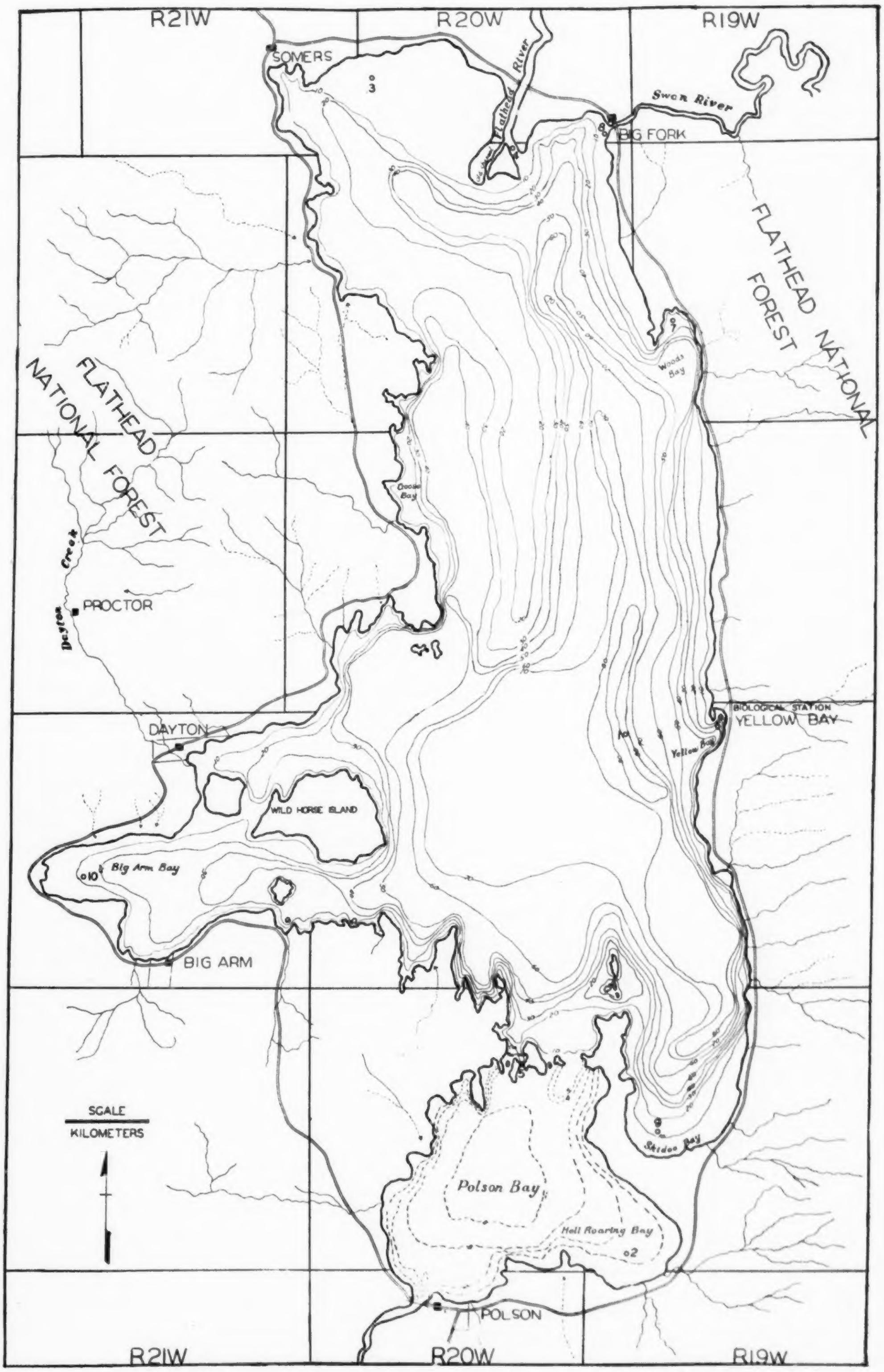

FIG. 1. Map of Flathead Lake from Graham and Young (1934) Depths in Meters. Locations of the Collecting Stations (1-10) indicated by circles.

northeast of the lake. Formerly the river entered the lake a little west of its present mouth, but as a result of meandering the old channel has been abandoned and now remains as a pool, or series of pools connected with the lake at high water only.

The lake is also drained by the Flathead River which flows swiftly through a tortuous channel with many rapids and falls to enter the Clark's Fork of the Columbia near Paradise.

Flathead Valley, which has a due north and south trend, is approximately 130 km. long and 10 to 30 km. wide. The lake fills almost the entire valley width, the mountains rising abruptly from the surface of the water at many points.

On the west side of the valley the mountains are lower, more rounded, and more extensively and deeply dissected by valleys than on the east side; where they rise sharply to form one of the most conspicuous and spectacular escarpments or mountain walls in the United States.

The accompanying map (Fig. 1) from the U. S. Land Office shows the general topography of the lake and its depths, which were located approximately by compass readings on prominent points of the lake shore, or in the case of those close to shore, by means of a measured line run from a boat to the shore. None of the locations pretend to be very accurate, but were the best that we could do with the time and means at our disposal, and give a sufficiently good idea of the lake contours. On a map of this scale (1:270,000) a variation of even 100 m. is inappreciable. As shown by the map the deepest portion of Flathead Lake is a rather narrow channel about 24 km. long and 4 km. wide, near the east shore, an arm of which extends westward to the mouth of Big Arm Bay.

The main body of the lake is from 30 to 75 m. deep, but the north and south ends are relatively shallow, having been partly filled with sediment. Its greatest depth is about 100 m. varying of course with the water level.

During the Glacial Age, Flathead Valley was nearly filled with a huge valley glacier, fed from the north and from mountain glaciers on the east and perhaps on the west as well. The valley was filled to a height of about 800 m. above the present lake level and rocky ledges below that elevation have been smoothed and rounded by glacial scour. On the retreat of the glaciers Flathead Valley and the larger tributary valleys were partly filled with glacial drift and sands and silt deposited by streams from the melting glaciers, which built a terminal moraine 138 m. high at the foot of the present lake, and through which the present river has cut its way to bed rock.

The length of the shore line, not including the islands, is approximately 185 km. about 55 km. of which are mud or sand, 50 of rocky and pebbly beach in the bays, and the remainder rocky cliffs. The rocks of the shore are quartzites, argillites and limestones. The erosion of the latter, which is more uneven than that of the others, has resulted in the formation of numer-

ous little headlands, and small islands, especially near the southern end of the lake.

The area of the basin drained through Flathead Lake, chiefly by Flathead River and its three forks, is 18,000 sq. km. The amount of water flowing annually through the lake varies from 80 to 120,000,000 cu. m., averaging about 100,000,000 cu. m.

Since 1907 the U. S. Geological Survey has maintained river gauges on the principal tributaries and the outlet of Flathead Lake. From 1907 to 1925 the maximum discharge was 2325 cu. m. per second on June 13, 1913 and the minimum 38. 5 cu. m. per second on March 14, 1920, while the rise and fall of the lake from 1908 to 1928 ranged from a maximum of 4.27 in 1913 to a minimum of 1.49 m. in 1915.[3] High water usually occurs in May or June and low water in February or March.

The supply of the lake comes chiefly from the numerous alpine lakes at the sources of the Flathead and Swan rivers, many of which are fed by the glaciers and snow banks of Glacier Park, an area of high and rugged mountains about 80 km. northeast of the lake.

Most of the surrounding region is wooded, but portions of the drift covered plain of the upper and lower valley and around Big Arm has been cleared, or are treeless. Some of the steeper neighboring slopes have been cleared for a short distance from the lake for fruit and vegetable farms.

BOTTOM DEPOSITS

Around much of the lake large rocks extend for varying distances from shore, being succeeded by gravel of gradually diminishing size, and this in turn by the almost impalpable ooze, which covers most of the lake bottom. In general the rocks and gravel extend to a depth of about 30 m. but this depth is of course very variable. In certain places, i.e. at the north and south ends of the lake and to a less extent elsewhere, the rock and gravel bottom is replaced by sand, or the ooze may extend to the shore, while the floor of the bays may be covered to a considerable extent by sunken logs and woody fragments.

The ooze, which covers so much of the lake floor, is composed of fine particles of sand, clay and organic detritus ranging in size from 10 to less than 1μ. Diatoms, both living and dead, are common, especially in the bays, together with pollen and various plant fragments of an indeterminate nature. Its color varies from point to point, dependent on the character of the adjacent shores and the method of its deposition, ranging from blue gray or brownish to a dirty yellow. In some places the color may change rather abruptly in the same area and in different layers, but to what extent minor currents may be responsible for this is unknown.

No chemical analyses of the ooze have been made, but no H_2S has been

[3] Elrod (1901) reports a rise of 5.8m. in one season.

found in the bottom water, while increase of CO_2 and decrease of O_2 near the bottom are not pronounced; so it is evident that decay is not active here. This is to be expected, from the low temperature and the scarcity of bacteria in the lower levels of the lake, as described by Graham and Young (1934).

CLIMATE

Flathead Lake lies in a region of low rainfall and moderate temperature. Records of the U. S. Weather Bureau (to 1933) at Kalispell, 16 km. north of the lake, show a mean annual temperature of 6.0°C for a period of 34 years, while at Polson, on the southern shore of the lake, the mean annual temperature for a period of 20 years was 7.2°. Absolute maximum and minimum at Kalispell are 37.2° and —36.7°, and at Polson, 40° and —31.1° respectively.

The average annual rainfall at Kalispell is 37 cm. and at Polson 39 cm., with a maximum and minimum of 49 and 26 cm. at Kalispell and 53 and 26 at Polson respectively, while the average number of sunny days (at least 75% sunshine) is 97 at Kalispell and 149 at Polson.

The average annual snowfall at Kalispell is 111 cm., the heaviest average monthly fall being 27.5 cm. in January and the lightest a trace in July with absence of snow in August only. At Polson the average is 113 cm. with a maximum average of 32 cm. in January, and none in May, July and August.

Total wind movement at Kalispell for 32 years was 67277 km. per year, with a maximum velocity of 64 km. per hour. The windiest months are April, May and June. There are no data on wind movement at Polson.

Prevailing wind directions are northwest at Kalispell and southwest at Polson. Apparently the slightly higher temperature over the lake than in the surrounding region creates an upward draft, causing wind drift from both north and south, with a rising air current over the lake and counter currents at higher levels. Since there are no data for wind movement at various points on the lake and at higher levels in the mountains it is impossible to test this hypothesis.

PHYSICS—LIGHT

The penetration of light in lakes is measured in various ways. The simplest and most generally used method is that of the Secchi disk, which is relative only and involves a personal factor.

Another method depends upon the use of photographic plates or films. Such a method is open to the objection that different emulsions have different sensitivities, not only in degree (speed) but also in quality (with reference to the spectrum). It is further subject to the limitation that in comparing any two intensities of light it is necessary that the densities and times of exposure be the same.[4] Therefore it is necessary to compare the intensities

[4] See Klugh (1925).

by means of screens of known transmissions placed over the sensitive plate or film. Such a method involves considerable technical difficulty and expense, and has not, as yet, come into general use, although several workers have recently employed it.[5] In a third method certain chemical substances, such as uranyl oxalate, enclosed in tubes of glass or quartz, are exposed to light at various depths and the rate of decomposition noted. This method has recently been used by Atkins and Poole (1930) in comparison with the photo-electric, or fourth method, to be described below. These authors found that with glass tubes the average ratio between the absorption coefficients, photo-chemically determined, and those determined by the photo-electric cell was 1.1 :1.0.

A fourth method involves the use of various electrical devices. Regnard (1891) used a selenium cell and galvanometer for this purpose, the resistance of the selenium varying with the intensity of the light. Birge and Juday (1930), in their work on the Wisconsin lakes and elsewhere, have employed the pyrlimnometer, which measures the heat effect of light by means of a thermopile; while Shelford and his colleagues,[6] and Poole and Atkins (1925) etc. have used the photo-electric cell.

The sensitivity of this cell varies with the kind of metal employed, whether the latter is mounted in gas or vacuo, on the kind of glass in the window of the cell, on the diameter of the latter, and on many other conditions, the details of which cannot be given here. The cell furthermore is relatively insensitive to red light.

In our own work on Flathead Lake we have employed the Secchi disk, photographic plates and filters and the Kunz photo-electric cell described by Shelford and Gail (*l.c.*). The latter has been adapted to our purpose and operated by Dr. G. D. Schallenberger of the Dept. of Physics of the University.

In operating the Kunz cell in 1928 and 1929, Dr. Shallenberger employed a 10 m. launch which was sufficiently stable on quiet days for this purpose. Due to difficulties of construction and operation—the latter depending on conditions of wind and sky—but few satisfactory sets of determinations have been made with this instrument, three of which are shown in Table 1 and Fig. 2.

A comparison of these results with those of Shelford and Gail (*l.c.*) on Puget Sound, shows a rather close agreement down to the 10 m. level, but below this they diverge widely. At 50 m. the latter found an illumination of 1,388 m.c.[7] or about 1.5% of 93,100 m.c.[8] in air, while the former's results show only 7.8 m.c.[9] at 50m., or .01% of the 72,600 m.c.[9] reading in air on the same dates. I can only surmise the reason for this difference since I

[5] Klugh (l.c. and 1927), Lönnerblad, (1929), and Oberdorfer (1929).
[6] Shelford and Gail (1922), and Shelford and Kunz (1926).
[7] Mean of 5 readings.
[8] Mean of 16 readings.
[9] Mean of 4 readings.

have insufficient data for Puget Sound water to compare with our own data for Flathead Lake. Probably the difference is due to larger quantities of plancton in the latter, but of this I have no information. Whipple (1927) gives the limit of visibility of the Secchi disk as 59 m. in the "Pacific Ocean", but for a body of water of that size such data are rather indefinite, and whether they apply to Puget Sound or not is not known. It is evident, however, from all the data available that sea water is in general much clearer than fresh

TABLE 1

LIGHT PENETRATION IN METER CANDLES AT STATION 1 ON THE DATES AND AT THE TIMES RECORDED.

Sun = reading in air.
Water = reading in water at the given depth. The 0 reading is with the cell just below the surface.
Ratio = the fraction of light transmitted by each 3 m. layer.

Observation No. 1. August 20, 1928.

Depth	Time	Sun	Water	Ratio
0	9:52	45,800	34,000	.72
3	9:53	46,100	14,600	.43
6	9:54	46,100	6,170	.42
9	9:54	46,100	3,900	.63
12	9:56	46,100	2,100	.54
15	9:57	47,200	1,240	.59
18	9:58	47,200	775	.62
21	9:59	47,700	325	.42
24	10:00	47,700	207	.64
27	10:01	47,700	128	.63
31	10:02	47,700	68.7	.54
34	10:03	47,700	41.5	.60

TABLE 1

Observation No. 2. July 23, 1929.

Depth	Time	Sun	Water	Ratio
0	11:50	66,500	48,000	.73
3	11:52	66,500	22,000	.46
6	11:53	66,500	10,500	.48
9	11:54	66,500	6,500	.62
12	11:55	66,500	3,700	.57
15	11:55	66,500	2,400	.65
18	11:56	66,500	1,390	.58
21	11:57	66,500	765	.55
24	11:58	66,500	450	.59
27	12:00	66,500	265	.59
31	12:00	66,500	160	.60
34	12:01	67,500	92	.58
37	12:02	67,500	57	.62
40	12:03	67,500	36	.63
43	12:04	67,500	22	.61
46	12:05	67,500	13	.59
49	12:06	67,500	8	.62
52	12:07	67,500	4.5	.56
55	12:09	67,500	3.0	.67
85 calc.	.....	......	.016248	...

TABLE 1
Observation No. 3. July 25, 1929.

Depth	Time	Sun	Water	Ratio
0	12:35	77,500	59,000	.76
3	12:33	77,500	29,000	.49
6	12:32	77,500	13,500	.46
9	12:32	77,500	8,100	.60
12	12:31	77,500	4,900	.60
15	12:31	77,500	3,000	.61
18	12:30	77,000	1,840	.61
21	12:30	77,000	1,000	.54
24	12:29	77,000	626	.63
27	12:28	77,000	397	.63
31	12:28	77,000	225	.57
34	12:27	77,500	140	.62
37	12:27	77,500	85	.61
40	12:26	77,500	55	.64
43	12:25	77,500	35	.64
46	12:25	77,500	20	.57
49	12:24	77,000	12	.60
52	12:23	77,000	7	.58
55	12:21	77,000	5	.71
58	12:20	77,000	3	.60
85 calc.	.....	......	.0228	...

water, which probably explains the difference in Shelford's and Shallenberger's results.

Poole and Atkins (1925, '26, '29 and '31) using photo-electric cells of various types obtained readings down to 70 m. in the English Channel. Their results average considerably higher than those of Shallenberger at depths of 50 m. and more, but on September 7, 1927 they record a transmission at 50 m. of only .0055%, which is somewhat less than the latter's results for Flathead Lake. The lowest illumination they record is 2.5 m.c. at 60 m. on the same date, while the lowest reading obtained in Flathead Lake was 3 m.c. at 58 m. on July 25, 1929. At 70 m. these authors found a transmission of 0.121% on May 7, 1928, while in Puget Sound Shelford and Gail (*l.c.*) record a reading of .01636% at 200 m.

Poole and Atkins (1928) have attempted to correlate Secchi disk readings with those obtained by means of the photo-electric cell, from which they conclude "that both the absolute and the percentage values of the illumination at which the disk was just visible varied widely. This was probably due to variations in the surface which would probably have a greater effect on the visibility of the disk than on the illumination." (*l.c.* p. 481). Their tables, however, show clearly that *in general* there *is* a positive correlation between visibility of the Secchi disk and transmission of light as measured by the photo-electric cell, as might be expected.

Oberdorfer (1929) employing a filter-wedge photometer gives a maximum transmission of 0.96% in March and a minimum of 0.11% in September

at 25 m. for Lake Constance. The maximum depth of visibility of the Secchi disk in this lake is given by Auerbach et al. (1924) as 16.7 m. in February.

Klugh (1927) with a similar type of apparatus found a penetration of 10% at 10m. in the Chamcook Lake, a clear water lake in New Brunswick, and 70% at 0.5 m.

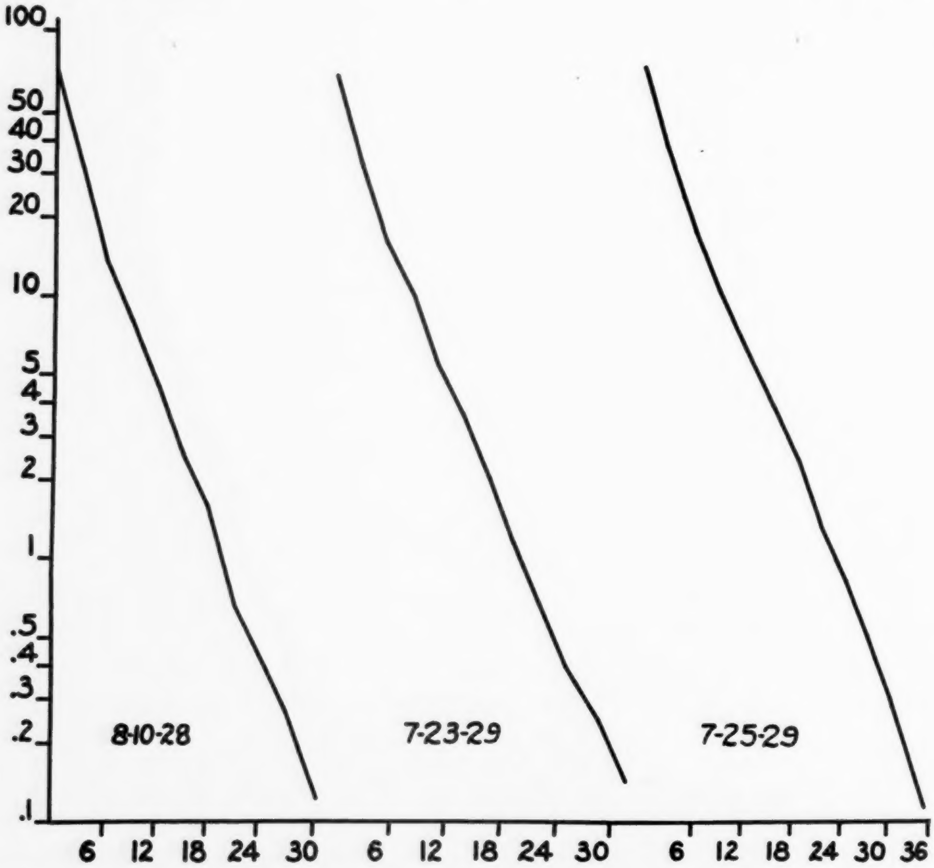

FIG. 2. Graphs showing penetration of light in Flathead Lake, plotted to a semi-logarhythmic scale. Depths are given as abscissae, percent of penetration as ordinates.

In Lake Mendota, Shelford and Kunz (1926) find a transmission of only 0.23% at 10 m.,[10] a result undoubtedly due to the large amount of plancton in this water; while Lönnerblad (1929) finds that in certain lakes of the Aneboda district in Sweden light penetration reaches a depth of only 6-7 m., a result which is doubtless due to the high color of these lakes from dissolved humus materials.

In general the results show a much higher penetration for Puget Sound waters than for the English Channel; or for inland waters generally. It is evident, both from these results, and from the Secchi disk readings above

[10] Computed from Table 1 in Shelford and Kunz (*l.c.*).

cited, that the former water is far more transparent than the other waters so far studied. An examination of clear deep lakes like Crater or Tahoe would be of much interest for comparison.

A glance at Table 1 will show that considerable variations exist in the percentages of light transmitted by different layers,[11] a result strictly in agreement with those of Shelford and others, and which is perhaps attributable to irregularities in vertical distribution of the plancton.

While it was impossible to obtain results with the photo-electric cell below 58 m., on the basis of results down to that point the calculated result for 85 m., the level at which most of our bottom plancton samples were taken, gives an estimated transmission of only .01818 m.c. or .000025%. As an approximate check on this result, I have made a comparison of the amount of light at 0:6 m. and at 85 m. by means of Cramer's "Spectrum process" plates covered with screens of varying densities, whose transmission percentages were determined in the Physics Laboratory of the University of Montana; the result of which, on October 18, 1931, gave a transmission at the lower level of .00007% of the light present at the higher level.

Assuming a transmission of 67% at 0.6 m., which is estimated from the results of Shelford and Gail, Poole and Atkins and Klugh and from those of Shallenberger on Flathead Lake, we should have a total transmission of .00007% x 67% or .000047% at 85 m. on this date; which result agrees fairly well with that of Shallenberger, considering that the former was determined in the autumn, when the water is much clearer than in July, when the latter was obtained.

A few determinations of light transmission in Flathead Lake have been made with the Secchi disk, a maximum reading of 13.2 m. being obtained on September 26, 1931, and a minimum of 4.5 m. on June 21, 1932. Under the ice in mid-winter I obtained a reading of 12.2 m. on February 3, 1930. The results are given in Table 2 which shows higher visibility in winter than in summer, a result which accords with those of other investigators, and is probably due primarily to the sediment which is deposited in the lake from the melting snows in spring and early summer and secondarily to the plancton maximum of this season.

TABLE 2. Visibility at different seasons in terms of depth of disappearance of a white disk (20 cm.) in diameter.

Date	Depth	Remarks
2/ 3/30	12.2 m.	Partly overcast sky, ice 15 cm. thick.
5/15/32	9.4 m.	Clear.
6/21/32	4.5 m.	Clear.
7/21/32	7.0 m.	Clear.
8/16/32	11.1 m.	Clear.
9/26/31	13.2 m.	Clear, but hazy.

[11] From 65.5% for the bottom to 46% for the upper 3m.

Judged on the basis of Secchi disk readings, Flathead Lake shows a penetrability intermediate between turbid lakes like Mendota and transparent lakes like Tahoe.[12]

As may be seen from the above brief summary of the work on the penetration of light in various waters, the problem is full of difficulties and the results are widely variable. Some of the difficulties involved are, first, those of a mechanical nature, such as obtaining a boat which is sufficiently steady for the use of delicate instruments (galvanometers), and water-proofing the electrical apparatus for work at great depths. Second, changes in the amount of light from the sky from moment to moment; variations which may not be visible to the eye, but which are nevertheless easily detected by delicate instruments. When clouds are passing across the sun the light intensity may vary from moment to moment by 100% or more. Thus in series 28 of Poole and Atkins (1929) the light in air varied from 73500 m.c. at 3.53 p.m. (4-19-28) to 25300 m.c. at 3.58 p.m. with the passage of a cloud. Third, changes in water surface may vary the light intensity by similarly great amounts, Shelford and Gail (*l.c.* p. 161) noting a variation from 67.3% to 26.0% in three minutes. A fourth difficulty, and one which is present in photometry in both air and water, is presented by the light angle and by the amount of reflection from glass surfaces. The effect of obliquity may be reduced or eliminated by the use of suitable diffusing glass windows (Poole and Atkins, 1929), but such windows absorb considerable amounts of light and thereby reduce the sensitivity of the apparatus.

We have little knowledge of the relative values of the direct and reflected light in water, but Poole and Atkins (1931) have found values of 0.22 to 0.61 for the ratio of the horizontal to the vertical light at depths between 0 and 30 m.

In relation to the biological significance of light in water, two considerations must be borne in mind. First, the total illumination, both in kind and intensity, is the factor which is effective in determining the growth, and therefore, abundance of photo-synthetic organisms; while, second, the direction of the light, in addition to its quality and intensity, is effective in determining the movement, and therefore distribution of phototropic types.

None of the data obtained thus far throw adequate light on either of these questions. They serve merely as a beginning in elucidating a most difficult, but interesting problem. They indicate, however, the extremely small quantities of light under which many organisms may live and enjoy active growth and reproduction.

The recent work of Hentschel (1928) and Schiller (1931) is of much interest in this connection. They found olive-green cells of uncertain relationship (Chroococcales or Chlorobocteriaceae?) at depths of 1200 m. in the

[12] Mendota, 1.75m. (Birge and Juday, 1911), Tahoe 33m. (Whipple, 1927).

Adriatic (Schiller) and even at 4000 m. in the Atlantic (Hentschel). Schiller is probably correct in his assumption that these cells may live in total darkness, for the maximum penetration of light which I have found recorded, is 1500 m., by Grein (1913).

Several turbidity tests have been made with the Jackson turbidimeter,[13] both in the open lake, the shallow bays and the mouth of the Flathead River, a maximum reading of 165 being obtained in the latter on May 14, 1932 when the river was in flood. No other reading has approached 25, the lowest recorded by this instrument. Heavy gales may, however, stir up the bottom of the shallow bays, rendering the water very turbid, but I have never made a reading at this time. A large amount of sand and silt is carried down by the Flathead River, and deposited on a sand bar, which extends many hundred metres from its mouth.

Early in 1916, a year of exceptionally high water, Dr. M. J. Elrod noted areas of very turbid water. In MS. notes he says "the blue, clear water usually ended abruptly at different places, changing to water of a dirty yellow into which (one) could see but a few inches." Similar conditions were observed on May 14, 1932 when there were numerous patches of very muddy water interspersed with clearer ones, extending some distance beyond the mouth of the Flathead River.

The color of the lake water is very faintly blue. The Flathead River, at least in early summer, is slightly brownish, giving a color value of between 10 and 15 p.p.m. on the platinum-cobalt scale of the American Public Health Association,[14] but we have never been able to get any readings on this scale in the lake itself. There is only a single reading, taken in Yellow Bay, in late summer or early fall of 1931, with Forel's standard.[15] This reading showed no sign of yellow in the water, for it failed to match a dilution of 5 ppm. of potassium chromate. Compared with an ammoniacal solution of copper sulphate, however, it matched a dilution of 25 ppm.

TEMPERATURE

The temperature cycle in Flathead Lake is similar to that in deep lakes elsewhere in the temperate zone, those having a well defined thermocline with a wide range of temperature at the surface and a small range at the bottom.

It is seldom that the lake freezes, except in the shallow bays, three exceptional years being 1929, 1930 and 1933. Our records include only the winters of 1929 and 1930 when the lake froze, but it is safe to assume that the winter temperature always reaches at least 4°C. at which point the period of winter stagnation occurs.

With the warming of the surface in spring an upper layer of warmer water, the epilimnion, gradually appears, separated from a lower, colder layer

[13] Whipple and Jackson (1900).
[14] Standard Methods of Water Analysis.
[15] Steuer (1910, p. 47).

by a well marked thermocline. The latter first appeared in 1929 shortly before May 18, or about a month after the ice left the lake.

From this time on the rapidly rising air temperature raises the temperature of the surface layer of the lake and the thermocline gradually descends, reaching a depth of about 30 m. by the middle of October and about 45 m. by the end of November. The rate of descent is not constant but varies apparently with the wind. The relation between the thermocline and the wind has not been adequately studied, however.

As the thermocline descends and the epilimnion gradually cools in the lowering temperature of autumn, the former slowly fades out, until, with the approach of winter, it entirely disappears and the circulation of top and bottom water is complete, with the temperature uniform from top to bottom. This condition was present on December 20, 1929 and probably for several days prior thereto.

There now ensues a period of inverse stratification, but without the establishment of a definite thermocline, due to the lowering temperature of winter cooling the surface water below 4°, the point of maximum density, while the lower layers are gradually and incompletely losing their heat by conduction.

TABLE 3. Variation of temperature with depth and time on September 9, 1928.

Time	Depth	Temperature	Wind and Sky
9:15 A.M.	0.0	15.3	Moderate north breeze, light sun.
9:20	1.5	15.4	
9:30	3.0	15.4	
9:40	4.5	15.4	Light cloud.
9:45	6.1	15.4	
9:55	9.1	15.3	
10:05	10.6	15.2	
10:20	12.2	15.15	
10:35	13.7	14.9	
10:40	15.2	14.2	
10:50	16.7	13.5	
11:00	18.3	12.5	
11:10	19.8	12.0	
11:20	21.3	10.8	
11:25	22.8	9.9	Light Sun
11:40	24.4	8.15	Part cloud.
11:50	25.9	7.6	
12:00 P.M.	27.4	8.1	
12:10	27.4	8.3	
12:15	27.4	8.4	
12:25	27.4	8.4	Fresh south wind, increasing in strength.
12:35	25.9	9.0	Rough sea.
12:45	30.5	8.0	
12:55	24.4	10.2	
1:05	60.9	5.6	
1:10	22.8	10.8	
2:10	94.0	4.6	
2:20	21.3	12.25	
3:50	0	15.4	High southwest wind.

Due to the changes briefly outlined above the surface temperature of Flathead Lake has an annual range of about 20° C. while that of the bottom (90 m.) is less than 3°. These relations are shown in figures 3, 3a and 6-9. The zigzag form of the curves, which is much more pronounced in the upper 30 m. than it is below 60 m. is evidence of the influence of the wind in creating currents in the lake, either directly, or by convection. The profound influence of wind on the distribution of temperature in a lake is beautifully shown in Fig. 50 in Whipple (*l.c.*), taken from observations by Watson on Loch Ness, Scotland, and has been discussed in detail by Kühl (1928) for the Walchensee in the Bavarian Alps. The inconstancy of temperature and the rapidity with which changes may occur are well shown in Kühl's Table 2, (*l.c.* p. 63) and in our own Table 3.

CURRENTS

Measurements of lake currents were made by Dr. Shallenberger with an instrument of his own device. He has supplied the following data.

While the general movement of the lake is necessarily from north to south it has not been possible to detect any current produced thereby except at Station 5, in the narrow channel between the islands at the entrance to Polson Bay at the southern end of the lake. The only currents found in the main body of the lake are those due undoubtedly to wind. In these there was considerable variation in direction and magnitude. On one occasion, following several days during which a strong wind blew from the south, a northward current was observed at station No. 1. This current had a value of 1200 m. per hour at the surface, and of 50 m. per hour at a depth of 15 m. Even at Station 5, where the main body of the lake flows through a channel about 100 m. wide and 15 m. deep, and where in calm weather the surface current is about 800 m. per hour southward, a northward current of 540 m. per hour may be caused by a strong south wind.

Table 4 shows how the current at Station 5 varied with depth on a calm day. Observations were made on August 10, 1929 on a southwardly directed current.

Table 5 shows how a northwardly directed current varied with depth on July 8, 1929, at Station 1.

Unfortunately there are no data on the thermocline for July 8, when the readings at Station 1 were taken. On July 12 it lay between 7.5 and 11 m. and was probably not much, if at all lower than this on July 8. Water movement must have extended therefore to a considerable depth below the thermocline, since the table shows it to have reached a depth of at least 15 m.

These results, obtained in summer, may not give even approximations of the maximum wind effect on currents throughout the year. They indicate in any case, however, the importance of wind in disturbing the surface layers

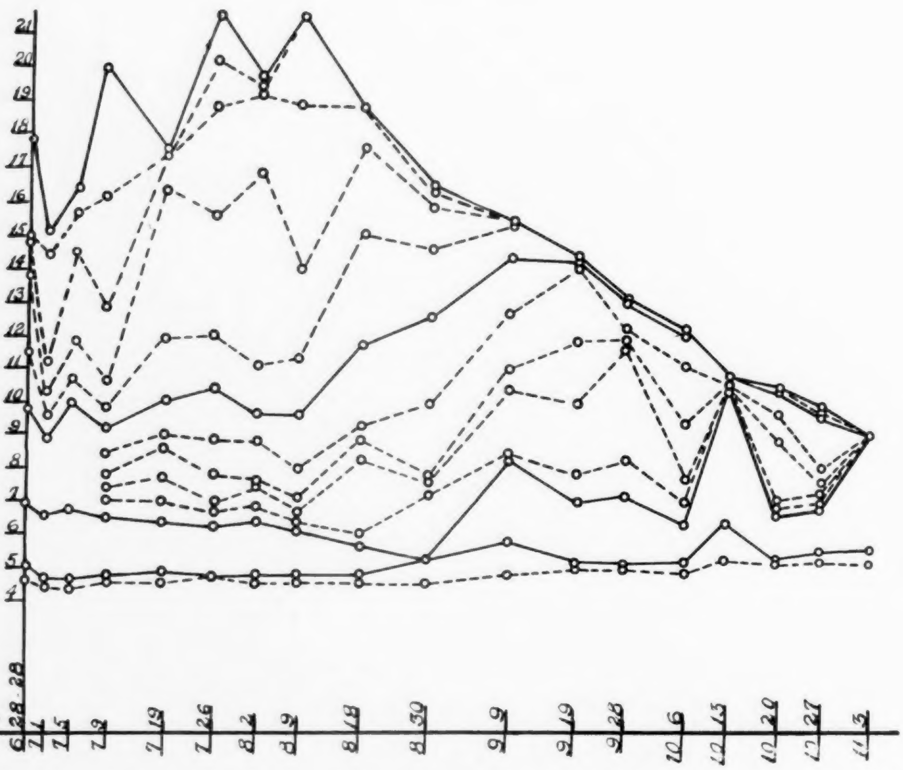

FIG. 3. Seasonal distribution of temperature. 1° C. = 1 division of the vertical scale. Temperatures at 0, 15, 31, and 61 m. are shown as full lines, while those at intervening depths are shown as broken lines. The bottom temperatures (85-91 m.) are shown as a single line. The slight variation between these depths is negligible.

of the lake down to a depth of at least 15 m., and thereby undoubtedly influencing the vertical distribution of temperature, gases and plancton in the lake. At the average rate of movement in the upper 2 m. of the lake on July 8, 1929 (Table 5) a mass of water would move the entire length of the lake in about 30 hours. Any movement of the surface layer in one direction necessarily involves a return movement at lower levels. Since a strong wind may blow uninterruptedly for several days, the entire surface layer of the lake may be turned over several times in the course of a single storm, and its temperature and chemical and biological contents be materially affected thereby. As these observations are very fragmentary, they give only a general conception of what actually occurs.

TABLE 4

Depth in m.	Current in m. per hr.
0	800
1	540
2	400
3	240
4.5	80

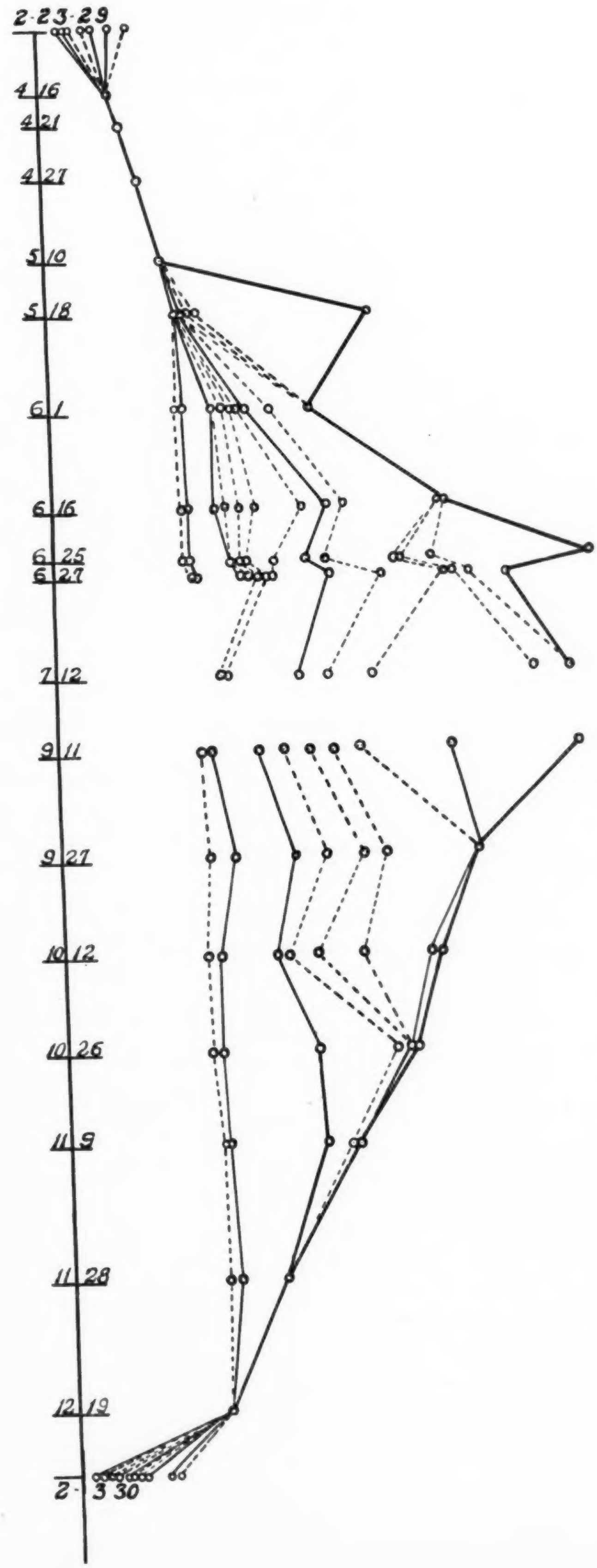

FIG. 3a

For description see Fig. 3.

A comparison of readings of the United States Geological Survey gauges at Somers and Polson show occasional differences in level of as much as 10 cm. at opposite ends of the lake. These differences may be due either to wind or inflow. They are, however, never large and probably exert a very minor influence on the life of the lake.

TABLE 5

Depth in m.	Current in km. per hr.
0	1.21
0.3	1.53
0.6	1.65
1.2	1.53
2.1	1.38
3.0	1.29
6.1	0.64
12.2	0.32
15.2	0.16

CHEMISTRY

Samples for chemical analysis were obtained with the Kemmerer water bottle (Kemmerer et al. 1923) until the loss of the latter, when a larger sampler designed by Dr. Shallenberger was substituted.

The chemical character of Flathead Lake is shown by the following analysis (Table 6) made by Dr. Howard. Samples for this analysis were taken at three widely separated points in the lake (Stations 1, 2 and 3). The results at all three points are practically identical. While this analysis indicates a water of high purity, it is not especially so, when compared with some other mountain lakes. Thus Lake Chelan in Washington, and Priest and Hayden lakes in Idaho have a total solid content which averages not much above 50% of that of Flathead Lake. On the other hand, when compared with other deep mountain lakes and with some European lakes, the total solid content is comparatively low. A comparison of twelve lakes is given in Table 7 which also shows their depths and the sources from which the data were obtained.

TABLE 6

Chemical analysis of Flathead Lake water in parts per million

Silicon Dioxide	8.2
Aluminum Oxide	9.38
Calcium Oxide	28.0
Magnesium Oxide	8.8
Chlorides	0.315
Nitrates	.0008
Sulfates	24.97
Sodium Oxide	0.865
Iron Oxide	0.016
Nitrites	0.000
Total solids	85.0

TABLE 7. Total solids of 12 lakes.

Location	Depth in meters	Total solids in parts pr. million.	Reference
MOUNTAIN LAKES			
Flathead, Montana	100	85	
Bear Lake, Idaho	55	1060	Kemmerer et al. (1923)
Hayden Lake, Idaho	58	52	"
Lake Pend Oreille, Idaho	366	146	"
Priest Lake, Idaho	113	49	"
Lake Chelan, Washington	454	44	"
Teleckoje Lake, Altai Mountains	325	56-60	Lepneva (1931)
Lake Geneva, Switzerland	310	171	Thienemann (1925)
Lake of Halstatt, Austria	409	158	Steuer (1910)
PLAINS LAKES			
Lake Mendota, Wisconsin	25	157	Birge and Juday (1911)
Lake of Plön, Germany	60	208	Thienemann (1925)
Greifen, Switzerland	32	190	Guyer (1911)

The nitrogen content of water is one of the limiting factors of its life, since nitrogen is an important element in the food of both animals and plants. A direct relation, however, between the productivity of a lake and the amount of nitrogen present cannot always be demonstrated. Thus, according to Domogalla et al. (1925) in Lake Mendota there is no relation between the variation in amount of phytoplancton and of nitrogen, while Utermöhl (1925) claims that in a small lake in Holstein nitrogen (and phosphorus) are not limiting factors in the development of phytoplancton. There can be no question, however, of the importance of nitrogen as a factor in the productivity of water, even though its immediate role be obscured by the multiplicity of other factors which govern this productivity. The relation of phosphorus in this connection is likewise problematical. While some authors (i.e. Seligo, 1926, Atkins, 1923, '25, '26, and Atkins and Harris, 1924) maintain its importance, others, i.e. Juday et. al. (1928) Minder (1926), and Tressler and Domogalla (1931) question this.

Nitrogen analyses were made at five widely separated points on the lake during the summer of 1928, and one at the mouth of the Flathead River in June 1929, when the river was in flood. The latter analysis was made to determine the amount of food material brought into the lake by the melting snows and rains of early summer. These analyses were made on the unfiltered water and hence do not differentiate between the dissolved nitrogen and that present in the form of plancton. Birge and Juday (1926) have shown that in Lake Mendota the ratio between the former and the latter is about 9:1. The results, which are rather brief and wholly inadequate for a study of seasonal variations in nitrogen, are given in Table 8. They indicate a greater amount of free NH_3 at lower levels than at the surface of the lake, which may be due either to loss of this gas at the surface through evaporation, to con-

sumption by plants, or to oxidation to nitrites and nitrates and the absorption of the latter by algae and Protozoa. The absence of nitrites and nitrates indicates that if ammonia is oxidized to these compounds, they are used up as fast as formed and hence do not appear in the analyses. Direct use of ammonia by chlorophyl-bearing organisms has been claimed by Pütter (1909).*

TABLE 8. Nitrogen analysis in parts per million.

Location	Date	Organic N.	Free NH_3	NO_2	NO_3
Station 1 (Main Lake), surface	7/5/28	0.1548	0.062	0.0	0.0
Station 1 (Main Lake), 31 m.	"	0.138	0.108	0.0	0.0
Station 1 (Main Lake), 92 m.	"	0.138	0.108	0.0	0.0
Station 2 (Hell-Roaring Bay), surface	7/7/28	0.074	0.026	0.0	0.0
Station 5 (Narrows), surface	"	0.090	0.038	0.0	0.0
Station 5 (Narrows), 15 m.	"	0.132	0.048	0.0	0.0
Station 3 (Somers), surface	7/14/28	0.106	0.660	0.0	0.0
Station 4 (Mouth of Flathead River), surface	"	0.026	0.018	0.0	0.0
Station 4 (Mouth of Flathead River), surface	6/18/29	0.104	0.048	0.0	tr
Average	......	.107	.131	0.0	tr

According to the work of Domogalla et al. (1925) on Wisconsin lakes the ammonia, nitrites and nitrates, which "originate in all probability from the decomposition of organic forms of nitrogen contained in the mud and debris at the bottom of the lake" (*l.c.* p. 278), are more abundant in the lower than the higher levels except at the time of the spring and fall turn-overs, when the distribution of dissolved substances becomes uniform from top to bottom. A similar distribution of nitrates in Lake Zürich is described by Minder (1926), who attributes this to their consumption by the more abundant phytoplancton near the surface.

These results do not agree with those of Burkholder on Lake Erie (Fish, et al., 1928) where free NH_3 is 2.5 times greater at the surface than the bottom in mid-summer. Burkholder attributes this to bacterial action, but in Flathead Lake Graham and Young (1934) found no evidence of denitrifying bacteria at the surface, although they were active at lower levels.

The relatively large amount (0.66 ppm.) of free ammonia at Station 3 (July 14, 1928), may have been due to the presence of a log jam in the neighborhood.

The results obtained at the mouth of the Flathead River on July 14, 1928 and June 18, 1929, which show much larger amounts of organic nitrogen and free ammonia on the latter date, suggest the effect of surface drainage on the nitrogen content of the river, due to higher water from rain and melting snow in the mountains.

* Since this ms. went to press I have learned of some experiments of Dr. C. E. Zobell of the Scripps Institution of Oceanography, which demonstrate the direct utilization of NH_3 by various marine organisms (Nitschia, Chlorella, etc.)

A comparison of the nitrogen content of Flathead Lake with that in some other lakes is given in Table 9, which shows also the depths of these lakes and the sources of information.

TABLE 9. Comparative nitrogen analyses of 17 lakes in parts per million, based on one sample except as otherwise noted.

Lake	Depth	Organic N.	Free NH_3	NO_2	NO_3	References
Flathead........ average 9 samples unfiltered	100 m.	0.107	0.176	0.0	tr at mouth of Flathead River	
Erie............ average 32 samples	64	0.076	0.017	....	0.15	Fish, et al. (1929)
Mendota........	25	0.4794 average 13 samples	0.0743 average 6 samples	0.0146 average 42 samples	0.0769 average 47 samples	Domogalla, at al. (1925)
Bass............	7	....	....	0.002	0.0083	"
Devil's.......... average 3 samples	13	....	....	0.007	0.0108	"
Geneva.........	43	....	....	0.001	0.0275	"
Green........... average 2 samples	68	....	....	0.00185	0.0296	"
Kegonsa........	10	....	....	0.0	0.0211	"
Madeline........	5	....	....	0.0025	0.0154	"
Michigan........	265	....	....	0.0096	0.1041	"
Monona.........	22	....	....	0.0036	0.0509	"
Rock...........	20	....	....	0.0018	0.0313	"
Turtle..........	14	....	....	0.0042	0.0278	"
Waubesa........	11	....	....	0.0	0.0227	"
Wingra.........	4	....	....	0.0	0.040	"
Zurich..........	50	0.085	0.02	....	....	Guyer (1911)
Zurich (upper)...	......	....	....	....	0.8 ([16])	Minder (1926)
Zurich (lower)...	......	....	0.02	....	0.26 ([17])	Minder (1926)
Greifen.........	32	0.15	0.05	....	....	Guyer (1911)
Greifen.........	......	....	0.039 ([18])	....	0.08 ([18])	Minder (1926)

In comparison with the other lakes in this table it is evident that free ammonia runs considerably higher in Flathead Lake, while the nitrites and nitrates are absent, with the exception of a trace of the latter in one sample.

Two analyses of dissolved phosphate were made in March 1934 on samples of water taken near shore at widely separated points, both of which showed very slight traces of this material.

Hydrogen ion concentrations were determined by the electrometric method. The pH value of the lake water ranges from 8.21 to 8.63. This alkalinity is doubtless due to the limestone in the adjoining mountains, the source of the tributaries of the lake, coupled with the relatively small amount of decomposing material in the lake itself. Our results being limited to the summer of 1928, I can say nothing about seasonal changes in pH. There is no apparent difference in the values for surface and bottom water as is so evi-

[16] 1 sample.
[17] Average of 147 samples.
[18] Average of 8 samples.

dent in Lake Mendota (Juday et al. 1924), which is to be expected from the slight effect of the bottom ooze.

Oxygen and carbon dioxide content were determined in connection with each of the quantitative plancton determinations and are shown in Figures 4 and 6-9. These determinations were made from June 6, 1928 to February 3, 1930, with a break in winter, when very few collections were made, and in July 1929, when one water bottle was lost and consequently one series of readings omitted.

Oxygen distribution in Flathead Lake is similar to that in other oligotrophic lakes—Geneva, Switzerland; Tahoe, California; Seneca, New York; which have an abundance of the gas at all levels in all seasons; and differs distinctly from that in eutrophic lakes, such as the majority of plains lakes both here and abroad, in which oxygen in summer decreases markedly in the hypolimnion and may be entirely absent at the bottom.

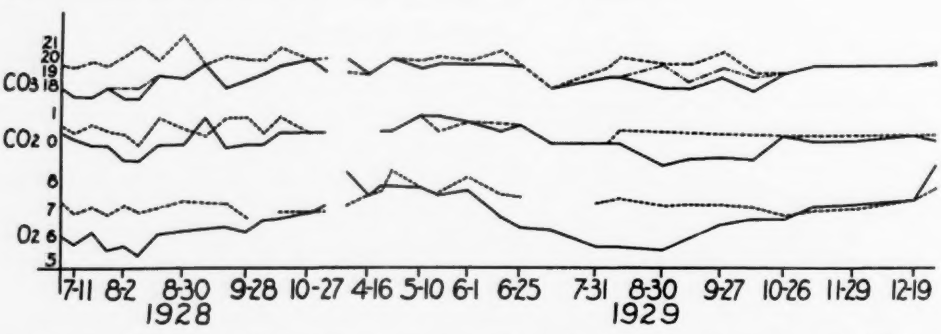

FIG. 4. Seasonal distribution of oxygen and carbon dioxide, in cc. p. l. plotted as ordinates. Dates are plotted as abscissae. The full lines indicate surface, and the dashes, bottom collections. Where the CO_3 and HCO_3 readings differ, the former is indicated by dots and dashes.

The dependence of the amount of oxygen upon temperature is clearly shown in a comparison of the curves for these two factors, for when the temperature decreases the amount of oxygen increases, and the bottom water contains a larger amount than the surface in summer, corresponding to the lower temperature there. Near the bottom, however, there is frequently a small decrease in oxygen due, undoubtedly, to decomposition (oxidation) of bottom ooze. This slight decrease, however, does not materially affect the total amount of oxygen, or its distribution in the lake, which is here determined primarily by temperature. In the Lake of Zurich, Minder's (*l.c.*) curves show a marked decrease of oxygen in summer from the surface to about 30 m., with some increase from there to the bottom. This is not explained by him, but is probably due, in part, to accumulation of zoöplancton in the thermocline and its decrease toward the bottom.

In the Attersee (Haempel, 1926) the bottom conditions apparently vary from time to time, as some of Haempel's curves show an increase, and others a decrease at this level. In winter, with the cooling of the surface as com-

pared with the bottom, the oxygen becomes higher in the former, than in the latter layer.

Organic activities (respiration, photosynthesis and decomposition) appear to play a relatively minor role in determining the oxygen content of Flathead Lake. However, a conspicuous instance of an increase in oxygen, due evidently to photosynthesis, is afforded by the data for August 9, 1928, when there was 0.2 cc. more at the 9 and 13 m. levels than at 16 m., because of a large development of Fragilaria at the former depths. This condition is similar to that recorded by Birge and Juday (1911) in Lake Mendota on September 20 and 21, 1908, and in Beasley, Long and Rainbow lakes in the summer of 1909 (l.c., Table 7, p. 43, and pls. 4, 5 and 6). It has also been described by Haempel (1926) and is evidently a rather common occurrence. We have, however, observed it only once.

During the vernal and autumnal periods of circulation, with equality in temperature between top and bottom, the oxygen is equal at the two levels for a short time at least. In Lake Mendota (*fide* Birge and Juday, *l.c.*) the surface oxygen undergoes a marked decrease in autumn due to (1) decrease in amount of phytoplancton, (2) active decay and (3) mixing of the oxygen-poor water below the thermocline with the water above, as the latter sinks, due to lowering temperature. This condition is not realized in Flathead Lake, which is further evidence of the relatively small part played by the organisms of the lake in determining its oxygen content.

Distribution of carbon dioxide (free, bound and half-bound) is shown in Figures 4 and 6-9. During spring and fall overturns there is uniformity from surface to bottom, with alkalinity developing at the surface in summer and fall, while the bottom is generally acid. The difference between these two layers in Flathead Lake, however, is rarely more than 1cc. per l., while in eutrophic lakes it may amount to as much as 50 cc.[19]

An unusual condition developed on September 9, 1928 when the surface showed 1 cc. of free CO_2 and the bottom only 0.5 cc. At intermediate depths (3-30 m.) the water was alkaline (Fig. 4). The explanation of this condition is not clear. At first I thought my results in error, but four readings all gave distinct, though small amounts of free CO_2 at the surface. On May 18, 1929, also, a single test showed more free CO_2 at the surface than at 85m. Similar conditions are shown by Birge and Juday (l.c., Figs. 10, 29 and 31) in Lake Mendota occasionally in winter and early spring and by Minder (l.c.) in Lake Zurich (June, 1921).

The alkalinity of the surface layer in summer is more marked in areas where vegetation is more abundant than elsewhere, as pointed out by Birge and Juday (*l.c.* p. 71). We have made no tests directly in these vegetation areas, but in Hell-Roaring Bay, at Station 2, near which is an extensive plant-grown area, in August 1928 alkalinity ran from 1 to 2 cc. of CO_2 pr. l.,

[19] Garvin Lake, Wis., 10/14/06, *fide*, Birge and Juday (*l.c.*)

while at Station 1 in the main lake it ran between 0 and 0.5 cc. at this time. Conversely, near the Somers's log boom, where thousands of logs are stored, free CO_2 runs considerably higher than elsewhere in the lake.

But little need be said regarding the distribution of the bound and half-bound CO_2. These are always equal in the lower strata of the lake and only rarely differ at the surface. They are equally distributed from top to bottom during the spring and fall overturn. During summer the amounts are usually a little lower (between 2 and 4 cc. pr. 1.) at the surface than at the bottom, while in winter there is a very slight difference (not more than 1 cc.) in favor of the surface water.

BIOLOGY—METHODS

Plancton samples were taken with the plancton trap described by Juday (1916). Thus far no one method has been devised which is wholly satisfactory for the collection and enumeration of plancton. The various methods employed have been discussed in detail elsewhere[20] and a summary of the objections to each has been given in a previous paper (Young, 1924). The trap was selected for the present investigation as most satisfactory; it is difficult, however, to compare the plancton productivity of Flathead Lake with that of other waters because other workers have usually employed the plancton net in their investigations. A comparison of the results obtained with trap and net indicates in general a considerably greater efficiency for the former.

In computing the amount of plancton various methods have been employed by previous investigators, which increases the difficulty of comparison between different waters. For a given investigation, however, where the same methods have been employed throughout, the results of the various collections are fairly comparative. Thus, while it is difficult to compare the amount of plancton in Flathead Lake with that in other lakes, the results for the former at different locations and levels of the lake, and at different seasons are fairly comparable with each other.

Our results are recorded in number of cells which, in the case of the colonial forms, makes them appear very high in comparison with those of other investigators.

Bottom samples for qualitative study were taken with a rake dredge, while for quantitative work a Birge-Eckman dredge covering an area of 1/16 m. was employed.

FLORA AND FAUNA

The flora of the lake includes several species of spermatophytes, the horsetail "fern" (Equisetum), the stonewort (Chara), one or more species of mosses and a large variety of diatoms, green and blue-green algae.

Omitting the very specialized parasitic fauna of the lake, its animal organ-

[20] Juday (1916), Reighard, in Ward and Whipple (1918), Steuer (1910) and Whipple (1927).

isms include representatives of every phylum, excepting a few, which are mainly, or exclusively marine.

The fauna is represented chiefly by protozoans, rotifers, nematodes, annelids, crustaceans, insects, molluscs and fishes; sponges hydroids, flatworms, bryozoans and mites being present in minor numbers, which, with an occasional tardigrade and gastrotrich and a few frogs, toads, turtles and muskrats, comprise the animal population of the lake.

I shall not attempt to give a detailed annotated list of species (amounting to some 700 in number), partly because of limitation of space, and partly because of incomplete identification of our collections, which comprise a number of uncertain and probably undescribed species. I shall attempt rather to indicate the salient features in the life of the lake as presented by the abundance and distribution of its characteristic forms.

BIOLOGICAL REGIONS

Without attempting to differentiate too finely between the various communities of the lake we may distinguish two main biological regions—the shallow bays and the open lake, which may, in turn, be subdivided into the littoral, pelagic and benthic areas.

A distinction between the various regions in a lake (littoral, sub-littoral pelagic, benthic and profundal) is difficult, not only because of the intergrading of the regions themselves, but also because of confusion in terminology of various authors.

The littoral as understood herein, is the region extending from the water's edge to a depth of approximately 10 m., i.e. to the limit of the larger vegetation (Potamogeton, Sagittaria, Chara etc.); the pelagic includes the remainder of the lake, while the benthic is the entire bottom, regardless of depth.

THE PELAGIC AREA

In this region may be included the major area of the deep bays with rocky shores, such as Woods and Yellow Bays in which the depth increases rapidly and conditions become very similar to those of the open lake a short distance from shore. The average depth of the open lake is about 50 m. It is a region frequently disturbed by wind in the upper layers. The exact depth to which this disturbance extends is not known, but from rather sudden changes in the level of the thermocline in summer, and from the depth at which currents may be detected, it appears to reach about 16 m.*

THE PLANCTON

The plants of the pelagic zone are almost entirely diatoms of the genera Asterionella, Fragilaria, Meloseira, Rhizosolenia, Synedra and Tabellaria

* See page 107.

with an occasional admixture of Cyclotella, Navicula, Cymbella, Campylodiscus, Surirella, Gyrosigma, Sphinctocystis, and Eunotia. Occasionally other algae occur, but these are mostly too rare to have any material influence on the ecology of this region and hence have been omitted in the charts. Of the blue-green algae Aphanizomenon, Chroöcoccus, Gomphosphaeria, Gleotrichia, Anabena, Aphanocapsa, Microcystis, Merismopedia and Spirulina are occasionally taken in open water, while the green algae are even less frequent in this region, being represented by a few specimens of Oöcystis, Sphaerocystis, Pediastrum, Cosmarium and Staurastrum. Of those forms which occur only occasionally in the plancton Chroöcoccus and Aphanocapsa are most important but even these, especially the latter, are too infrequent to play an important part.

The animals of the open lake include a limited number of common species with an admixture of several infrequent types. These are mainly flagellates, rotifers, copepods and cladocerans, with a few rhizopods and ciliates,[21] and rarely a dipterous larva, the latter probably a wanderer from the benthos. At least 90% of the animals of this region are the flagellates Ceratium and Dinobryon; the rotifers, Asplanchna, Gastropus, Notholca, Anuraea and Polyarthra; the copepods, Cyclops and Diaptomus; and the cladocerans Daphnia and Bosmina; with a few Epischura, Sida, Leptodora and very rarely Canthocamptus.

The presence of shell-bearing forms like Difflugia and Centropyxis in the plancton is interesting, since such organisms are not active swimmers and possess no obvious means of flotation. It is probable, as suggested by Steuer (*l.c.,* p. 103), that they form vacuoles of gas which decrease their specific gravity. Cyphoderia has been found in several collections from points of intermediate depth (15-21 m.) at Stations 5, 6 and 9, but always near the bottom; so that it is almost certain that this is a bottom form, which has been accidentally brought into the plancton by currents created in raising or lowering the plancton trap.

It is difficult if not impossible to arrange this assemblage in the order of dominance. The importance of any organism in the household of nature is primarily a matter of food; on the one hand, the amount which the organism consumes, and on the other, the amount which it supplies for other species. This, in turn, depends both on the abundance of the species and on its size and rate of metabolism. Regarding this last factor we know very little, though it is obvious that the more active the organism the higher will be its metabolic rate.

The lack of any quantitative collections from the areas where plants are most abundant renders it difficult or impossible to determine the relative abundance of the great majority of species in Flathead Lake. Moreover, many of them are attached or crawling forms, and there is no known method of com-

[21] Commensals on Crustacea.

paring their abundance with that of pelagic types. The best we can do, therefore, is to compare the relative frequency of various organisms in collections made in different localities at many times. By this means, and by size comparisons it is possible to draw some very general conclusions regarding the relative importance of different species in the economy of the lake.

In such a comparison perhaps *Cyclops bicuspidatus* should be given first place, although during summer and fall *Daphnia hyalina* may outrank it, because of its greater size. While the rotifers outrank the Crustacea by nearly 2:1 and the Protozoa outrank them by 500:1 in number of individuals, their greatly inferior size probably makes them of less importance in the life of the lake.

The seasonal distribution of the plancton has been studied mainly at Station 1, located at a point about 2 km. from the mouth of Yellow Bay in a depth of over 90 m. at high water. A number of collections to determine differences in regional distribution have been made at the nine other stations, but extensive seasonal studies have been made only at Station 1. The composition of the plancton and the depth distribution of its constituent forms is similar at all points studied, with the exception of Station 4 in the mouth of the Flathead River, which has a very different environment from the others.

It should be said at the outset of any discussion of seasonal distribution of the plancton that our results cover only nineteen months, from July 1928 to February 1930, while from November 3, 1928 to April 16, 1929 but one series of collections was made on February 23. A comparison of the abundance of plancton in different years must necessarily, therefore, be very incomplete. However, our 1928 collections show somewhat smaller results than do those of 1929 for the same seasons. Such a result is entirely in accord with the results of other workers. Thus Birge (1897), p. 317 says, "The feature of the annual distribution of the Crustacea which surprised me most in the progress of my work is the great difference between the numbers of the same species of Crustacea present in successive years. I do not refer so much to the larger or smaller numbers of forms like Cyclops for whose variations causes can be assigned at least in part, but rather to such facts as those shown by *Daphnia retrocurva* and by Diaphanosoma, which are either absent or present in very small numbers in one season and appear in great numbers in another year. For such variations it is very difficult to assign even conjectural causes.

"A similar fact has appeared in the succession of the algae. It is not true for Lake Mendota that the forms of algae succeed one another in a definite order in successive seasons so that one can be sure of finding certain forms at certain times of year, as would be the case with plants of woodland or prairie."

In comparing the amount of plancton at different seasons, moreover, it must be borne in mind that in computing most of our averages we have used

12 samples taken at the surface, at 1.5, 3, and at each succeeding 3 m. interval down to 31 m., and two samples at 61 and 85. m. respectively.[22] The upper 30 m. of the lake contains most of the plancton during most of the year and is the region of the greatest changes in temperature and light. But this method does not give results which are strictly comparable to each other unless the depth distribution is uniform, which it is, approximately, only in winter and spring. During the remainder of the year, when there is a higher concentration of plancton in the upper 30 m., this method raises the average as compared with that during the former season. To this discrepancy Kühl (*l.c.*, p. 143) has already called attention.

As already noted* diatoms are of chief importance in the study of the phytoplancton. The chart (Fig. 5) shows two well-marked maxima in 1929, one in May-June and the other in November-December. In 1928 the numbers were much lower on the average than in 1929, and the peaks in the curve less well defined. In this year diatoms were more numerous in August than at other seasons, with a minor rise indicated in October-November.

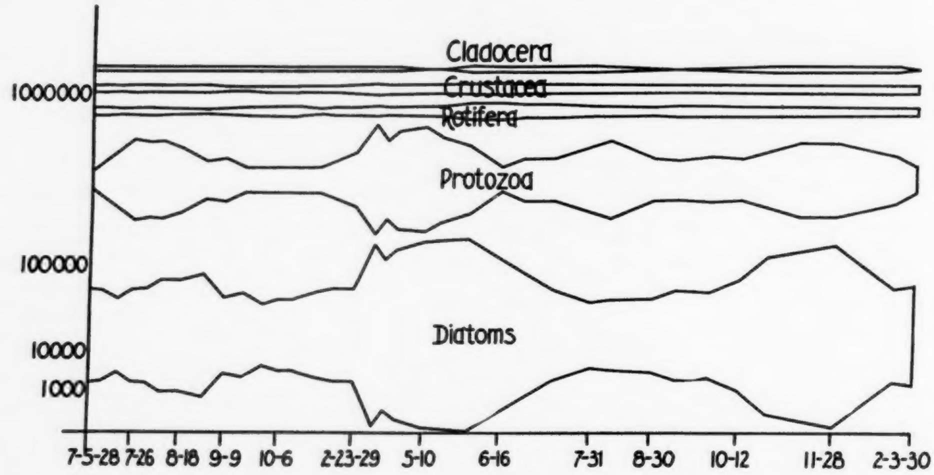

FIG. 5. Seasonal distribution of plancton. The dates are given on the horizontal, the number of organisms pr. l. on the vertical scale, which is plotted as the cube root of the latter.

Most of the diatoms are perennial, with a period of maximum development in April-June, while some (*Melosira crenulatum*, Tabellaria and Synedra) have a secondary maximum in summer or early autumn. *Fragilaria crotonesis*, however, has its major maximum in summer or autumn, with a minor maximum in spring. In 1928 it reached its peak at 12 m. on August 18, with 110,000 cells pr. l. In November of this year it had a second, smaller development, with a peak of 54,000 cells pr. l. at 6 m. at Station 6 on November 18. In 1929 it reached a peak of 30,000 cells pr. l. at 61 m. May 18, and one of 310,000 pr. l., also at 61 m., on November 28.

[22] Depths were originally measured in feet. In changing to metres, I have given the nearest integer.

* See page 117.

The autumn rise in the diatom curve for this year, and the mid-summer maximum in 1928 are due to the abundance of Fragilaria at these seasons.

Rhizosolenia is another aberrant genus in respect to its seasonal distribution. Very common during the summer of 1928 it reached a maximum of 51,000 pr. l. at 18 m. on July 26, disappearing late in September to reappear in early November. It was fairly common during June 1929, with a maximum of 10,000 pr. l. at 27 m. on June 1. After June it was usually present in scanty numbers until the following February when the work ended.

Also unlike most of the plancton Chroöcoccus has its maximum in the autumn. There are a few scattered records prior to July 31, 1929 when it became relatively common, with two fairly well defined maxima, on August 30 (11,000 pr. l. at 18 m.) and November 28 (9,500 pr. l. at 12 and 30 m.) respectively, and an intervening low point on October 12. Whether these two maxima are significant is uncertain. Further records would be required to determine this. It is interesting to note that on August 10 Chroöcoccus was high at the surface of the Flathead River near its mouth (10,500 cells pr. l.) This occurrence preceded the first maximum at Station 1 by about three weeks and very possibly contributed to it. It occurs mainly in the upper 30 m. of the lake.

Aphanocapsa is very sporadic in its occurrence, being scarcely noted in 1928, but was somewhat more frequent in 1929. Its distribution, both seasonal and vertical, is similar to that of Chroöcoccus but less regular. It reached a maximum of 8,000 pr. l. at 1.5 m. on September 11, 1929.

Considering the zoöplancton as a whole we note that the chart (fig. 5) of the seasonal distribution shows one well marked maximum in early summer with a secondary one in late autumn. In 1929 these occurred in mid June and November respectively. In 1928 our records began on July 5 and ended on November 3, so that the June and November maxima, if present, are not shown. There is, however, an indication of the latter on November 3. Early autumnal minima are shown in both years, on September 28, 1928 and October 2, 1929, with another minimum at some time in winter. While our winter records are too few to show the exact dates of the winter minimum, it is quite clear from the chart that such occurs. Besides these major waves there are several minor plancton oscillations, secondary maxima occurring in July and early October of 1929, and in April, May, July and September of 1929, with corresponding minima at intervening periods.

The major waves of zoöplancton in Flathead Lake are thus seen to correspond fairly closely with those recorded for lakes of a similar character elsewhere.* A satisfactory explanation of these yearly changes has yet to be given, but is doubtless to be found in the interaction of the many factors which determine the physical and chemical environment of the plancton. Temperature, light and food supply are unquestionably the controlling

* See page 123.

factors in plancton development, and these factors interact one with another in very complex fashion. Thus, the food supply of the zoöplancton is composed of bacteria, algae and members of the zoöplancton itself, as well as the organic content of the water in the case of saprozoic Protozoa.* The bacteria and algae in turn depend upon this organic content for food and this is furnished in part by animal excreta and by the decaying bodies of the animals themselves. Light determines, in large measure, the growth of algae and thus contributes to the food of the zoöplancton.

The basis of the food supply is the carbon and nitrogen dissolved in the water. There appears to be an ample supply of HCO_3 present at all times for the phytoplancton, and, probably N as NH_3 is always present in small amounts; but, as already indicated, our results are too fragmentary to tell much about the latter element. Oxygen is abundant at all seasons and hence need not be considered here. Temperature and light are probably the major factors in producing the spring increase, and it is possible that they also determine the increase in the fall. In spring and fall it is not unlikely that these factors reach their optimum. With increasing clearness of the water, light penetration reaches its maximum in the fall,** while in summer the high temperature is probably unfavorable for the diatoms, which accordingly decrease in number, with resultant decrease in the animals which feed upon them. In 1929 the maximum of the diatoms and Protozoa occurred in April-May being succeeded by that of the Metazoa in June; while the Protozoa minimum in June and that of the diatoms in July-August was followed by that of the Metazoa in late August. The poorly marked maximum of the Metazoa in November of this year coincides closely with better marked maxima of the Protista at this time. In 1928 the curves of the Protozoa and the diatoms follow each other rather closely and the same is true in the spring and fall of 1929, but in August of this year there was a well marked minor maximum of the Protozoa coincident with the mid-summer minimum of the diatoms.[23]

It is generally assumed that the metazoan plancton uses the phytoplancton for food. This assumption has, however, been questioned by Naumann (1921) and others, who assume, either that the zoöplancton and even fishes (Kostomarov, 1928) absorb nutriment from the water, or that organic detritus serves as food. Kühl (*l.c.*, p. 144) has discussed this question in some detail, and I shall not consider it here further than to emphasize the fact that our knowledge of the food relations of the plancton at present is too inadequate to enable us to draw any certain conclusion regarding the dependence of one form upon another in the seasonal cycle. Furthermore, it is not unlikely that the factor or factors determining abundance at one season are different from

* See page 112.
** See page 103.
[23] This discussion is based on the distribution of Dinobryon, which, in respect to cells, far outnumbers all the rest of the Protozoa. The distribution of Ceratium and Difflugia is still different, while Peridinium and Mallomonas, the other two principal Protozoa in the plancton are present in relatively insignificant numbers.

those which determine it at another. According to Thienemann (1926), Minder (1926) etc., Liebig's "law of the least" applies here; namely, that, given a number of factors (food, temperature, light, etc.), that factor which is least in amount is critical for the abundance of any species.

The seasonal distribution of fresh water diatoms has been discussed by Whipple (1927), who has pointed out the complicated nature of the problem, and the important relation of temperature, light and solutes (oxygen, nitrogen, etc.) to their development. According to this author diatom maxima occur in spring and fall during the periods of vertical circulation of the water, at which times dissolved food materials, as well as diatoms (or their spores) which have lain dormant at the bottom during winter and summer stagnation periods, are carried to the surface, where conditions of light and temperature are encountered which are favorable to the increase of diatoms. With cessation of circulation and subsequent stratification the diatoms gradually sink into lower regions, where conditions are less favorable for their growth, and there "remain dormant through another period of stagnation" (*l.c.*, p. 232).

A similar relation between periods of circulation and stagnation and the development of phytoplancton has been described by Lozeron (1902) and Minder (1926) for the Lake of Zurich. Bachmann (1911, p. 156), on the other hand, says regarding this theory that "Im Vierwaldstattersee und in den grossen südlichen Schweizerseen müssen wir nach andern Ursachen suchen, welche den Diatomeenmaxima zu grunde liegen." And Flück (1927, p. 40) agrees that there is "keinerlei Beeinflussung der vertikalen Verteilung durch diese Strömungen."

In Flathead Lake the seasonal distribution of diatoms agrees well with this theory; but their increase in August 1928 when the lake temperature was at a maximum and the thermocline was well established can not be explained in this manner. This increase was due, in part, at least to Rhizosolenia whose peculiar behavior has been discussed above.*

A di-cyclic type of plancton development has been noted by many authors in the Swiss lakes, while, according to Robert (1919), the Baltic lakes have a mono-cyclic type. The former are deep, cold lakes, the latter comparatively warm and shallow ones. Lake Mendota, however, (Birge, *l.c.*, and Birge and Juday, 1922) has a di-cyclic type, and the same is shown in the plancton curve given by Steuer (*l.c.*, p. 553, from Fuhrmann) for the lake of Plön in Germany. Both of these are lakes of the Baltic (eutrophic) type. So it is evident that no invariable relation can be established between the type of plancton development and the physical type of lake concerned.

The depth of lakes has an important influence on the life histories of their inhabitants. According to Wesenberg-Lund[24] certain species of rotifers reach

* See page 121.

[24] Fide Steuer (*l.c.* p. 296).

their maximum several weeks earlier in smaller lakes than in neighboring larger ones, and along the shores of the latter about a week earlier than in deeper parts. In my opinion this difference is due to temperature rather than to any direct effect of depth upon development.

The table given by Bachmann (1911, p. 154) shows the marked variations which may exist, not only between different species in the same lake, but also in the same species in different lakes in respect to the times of maximum development. While it is true that lakes of similar physical type show generally similar biological conditions, nevertheless each lake has its own individual character, comparable, in a way, to the individuality of the members of any biological group or "species".

A similar opinion relative to the bottom faunas of lakes is expressed by Lundbeck (1926, p. 186) who says: "Die Mannigfaltigkeit und Veränderlichkeit der einzelnen Faktoren können sich zu so zahlreichen Kombinationen zusammenschliessen, dass fast jeder See ein anderes Bild der Verteilung der Lebewesen des Bodens bietet." And Guyer (1911, p. 378) says: "Die obigen Vergleiche ergabern, dass in bezug auf das Eintreten der Maxima der verschiedenen Planktonten in den verschiedenen Seen grosse Unterschiede bestehen, und wenn wir die jeweiligen physikalischen Verhältnisse des Mediums ins Auge fassen, so finden wir, dass gerade die Temperatur der variabelste aller Faktoren ist und ganz ähnlich auch die Intensität des Lichtes ändert. Es fragt sich nun, ob wirklich so und so viele biologisch verschiedene Rassen einer und derselben Spezies existieren, oder ob nur die jeweiligen Unterschiede in der Beschaffenheit des Mediums die Änderung der Maximazeiten bedingen."

Another factor, of which we are deeply ignorant at present and which has accordingly received but scant consideration, is the length of life of plancton animals. The life span of any organism is, in general, though with many exceptions, proportional to its size.[25] "Needham and Lloyd (1916) state that 'the rotifer, Hydatina is said to have a length of life of some thirteen days', but give no authority for their statement. Steuer (*l.c.*, p. 269) gives the ages of a few copepods the average being 13 months. This figure appears high for the average life span of fresh water copepods. Judging from the curves for Devils Lake and for Lake Mendota and Green Lake, Wis., as given by Birge (1897) and Marsh (1898) the average is very much less than this. But the facts, so far as known at present, do not warrant any final conclusion." (Young 1924, pp. 45-6).

Walter (1922) describes two varieties of Cyclops viridis, one with a life span of 7-9 months and another with a span of 4-6 months, the males in each case being shorter-lived than the females. The former variety is hatched from November to February and the latter during the rest of the year. Probably

[25] See Minot (1908, p. 227).

the smaller copepods have a life span of 4-6 months, while Diaptomus vulgaris lives for 10-13 months.

Robert (1919), after reviewing the work of several authors, together with his own, reaches the conclusion (p. 41) that "Nous ne pensons pas qu'un seul des facteurs généralement invoqués: temperature, circulation ou stratifications des eaux, puisse a lui seul expliquer la date d'apparition des maxima et minima du plancton. Ceux-ci dependent sans doute de facteurs fort complexes et difficiles a isoler, parmi lesquels ceux que nous avons étudiés jouent probablement un certain role."

The above discussion, however, while offering some possible explanations for the major cycles of plancton development, will not explain the numerous minor fluctuations which appear in any yearly curve of plancton abundance. It is possible that these fluctuations are more apparent than real, due to errors in making or in counting the collections; or, which is more probable, to irregularities in distribution of the organisms themselves.

The horizontal distribution of the plancton has been studied by many authors with divergent results; but the general conclusion is that, barring occasional swarms, which are found chiefly among the Cladocera, and given similar environmental conditions, this distribution is reasonably uniform. Indeed the whole procedure of plancton study is based on this fundamental assumption. Numerous and large variations have been found, however, in both vertical and seasonal distribution of the zoöplancton by various investigators, which are more readily explained by the assumption of an irregular horizontal distribution than in any other way. Such an assumption does not, of course, imply that the horizontal distribution is *always* irregular but only that it *may* be so at times.

Examples of irregularity of vertical distribution are shown in the curves of the Crustacea and nauplii in Lake Mendota on September 8, 1896 (Birge, *l.c.*, Pl. 42). "According to these there were more adult Crustacea by about 35% at the 6 than at the 4 m. level, and slightly more at 3 than at 2 m., in spite of the fact that they were decreasing rapidly from above downward, except in the first half metre. The nauplii vice versa, while increasing from above downward, were nearly 50% fewer at the 4 than at the 3 m. level.

"Again consider the Diaptomus charts of Marsh (1898, Pl. 7). In August 1896 there occurred, according to the chart, two well marked maxima and minima with numbers ranging from 1563 to 3803,[26] a difference of nearly 150%. Similar, though less marked irregularities are shown in the curves of Birge (*l.c.*)" (Young, *l.c.*, pp. 42-3), and in those of the Wisconsin lakes given by Birge and Juday (1911) and the Finger Lakes of New York (*ibid.*, 1914). These authors consider them evidence of stratification of the organisms concerned. They deny the likelihood of their causation through errors in collection or counting, but apparently overlook the possibility of irregu-

[26] Total catch.

larity in horizontal distribution being responsible for an *apparent* irregularity in vertical distribution, nor do these authors attempt an explanation, merely contenting themselves with the statement that "such results . . . should be expected . . ." (1911, p. 116).

Behrens (1914) has shown the marked variation which may occur in the number of crustaceans occupying a given layer of water at different times, the number at night being from 200-400% higher than during the day. He attributes these differences to a retreat of these organisms to the bottom during the day time, but Kühl (*l.c.*, p. 139) attributes them on the contrary to "einer horizontal Wanderung der aktiven Schwimmer and zu dem mit passiven Transport durch Strömungen."

Marked irregularities in vertical distribution are also shown in the charts of Kemmerer et al. (1923). In Hayden Lake, Idaho, on July 7, 1911, for example, the Protozoa decreased from the surface to the 8 m. level, then suddenly increased at 10 m., with a minor decrease at 12 m. and a great increase at 15 m., with a decrease to the 40 m. level and a slight increase at 50 m. The crustaceans and diatoms also were equally erratic in their vertical distribution in these collections. Similar examples might be cited from studies of vertical distribution in any lake.

At first sight it might appear that there is no relation between irregularity in vertical and in horizontal distribution. However, it is quite evident that if the plancton *does* have an irregular horizontal distribution in the different strata of a lake and if, in a vertical series of collections one sample was taken in an area of denser population in one stratum, and another sample in one of sparser population in another stratum, then these differences in horizontal distribution might cause similar differences in vertical distribution.

A careful study of horizontal distribution of plancton in Devils Lake, N. D. has been made by Moberg (1918) who concludes that "(1) the zoöplancton in Devils Lake shows a great irregularity in horizontal distribution and this irregularity cannot be correlated with any variations in amount of phytoplancton or in the chemical and physical environment. It is more likely due to the habit of swarming among plancton animals, due perhaps to a social instinct, similar to that found in many other groups of the animal kingdom. Plancton swarms are at times visible even at considerable distances to the naked eye. (2) With larger samples (19 litres) the variations tend to be reduced, but even here they are at times greater than in the smaller ones (½ l.). (3) These variations invalidate the usual assumption that a given sample of water is representative of a large area, at least in respect to its animal inhabitants, and necessitate the collection of large numbers of samples before definite conclusions regarding their distribution or movement can be drawn." (*l.c.*, p. 264-5).

Gardiner (1931), however, in a comparison of 80 collections of Crustacea, made from a drifting ship at sea, found that 77% of them did not vary more

than ± 33% from the average, or a total range of not more than 66%, but occasional samples departed as much as 90% from the mean. This variation is considerably less than that found by Moberg (from 121% for Cyclops to 185% for Diaptomus in two series of samples of 19 l. each), and is more nearly in accord with the results of Apstein (1896) for the Dobersdorfer lake. Both Gardiner and Apstein, however, based their results on vertical hauls with a net, which would tend to obscure any possible variations in depth distribution. Thus Gandolfi-Hornyold and Almeroth (1915) found a range of variations of 242% in the distribution of Daphnia hyalina in Lake Geneva in vertical hauls from 10 m; but when the hauls were made from a depth of 20 to 30 m. the range of variation was reduced to less than 40%.

Recently Naber (1933), by means of mathematical analysis, has shown that the differences between the averages of two series of plancton collections, one taken at the same place, and the other at different points in the same lake, all samples of both series being taken within a period of 45 minutes, are less than 3 X the probable errors of the means. He concludes therefore that there was "keine Unregelmässigkeiten in der Horizontalverbreitung die über das bei Schwankungen an der gleichen stelle zu beachtende Mass hinausgehen" (*l.c.*, p. 128). Naber's figures however show clearly that the differences between the maxima and minima of each species studied and its mean were greater than 3 X the probable error in the series taken at different points; and the same was true in many, though not all of the collections at the same point. His results, therefore appear to support my contention that plancton distribution is not uniform under uniform conditions, as is so often assumed.

In collections of ostracods in laboratory jars I have noted a tendency of these organisms to collect in "swarms" or irregular masses on the sides of the jars, and similar cases are recorded by Allee (1931) in isopods (Asellus) and brittle stars (Ophioderma). The causes of these aggregates are manifold and obscure. "Social instinct", "prototaxis", "mass protection" and "biophysical integration" are some of the vague terms which have been used in "explanation", but it must be admitted that the whole question is very uncertain at present. Enough has, however, been done to throw much doubt on the generally accepted assumption of a uniform distribution of the plancton.

Irregularities of distribution are hardly adequate, however, to explain the abruptness of some of the changes in the curves. These abrupt changes are well illustrated in the diagrams of Birge and Juday (1922) (Figs. 28, 31, 34, 35) and in those of Young (1924) (Pls. 11-19, 21, 22). The fluctuations in the latter charts from counts made by the Sedgwick- Rafter method, using only 500 cc. samples, may be due in large measure to experimental error and to local variations in distribution; but those in the former, which were based on collections ranging in amount from 700-1500 l.+ for the centrifuged material and from 200 to 38,000 l. for the material strained by the net, are

hardly attributable to such factors. The collections being made at the same, or very closely adjacent points, variation in location will not explain the changes. Another possible explanation is the brevity of the life cycle and rapidity of growth of most plancton forms to which reference has already been made.*

Assuming a brief life cycle and rapid growth under favorable conditions, one can readily understand such large and sudden fluctuations as are shown in the figures above cited, and in our own figure 5, in which there was a sudden and large drop from the high point of April 16, 1929 to the low of April 21, with a subsequent rise from April 27 to May 10. In this case the curves represent an average of 14 samples of 25 l. each, taken at various depths from the surface to 85 m. Variations in horizontal distribution, all in the same direction, in the several groups of organisms represented are eliminated by the law of chance, and there was no constant wind during the period involved to possibly account for movement of the plancton as a whole, so that the only explanation apparent is the death of a large part of the organisms present on April 16 and the appearance of a new generation between April 21 and May 10.

As shown in Figure 5 the four major groups of zoöplancton roughly parallel each other in their annual distribution with, however, many minor variations. Each has its major maximum in April-June with a minor maximum in October-November, but the exact dates on which these occur naturally differ for each group, and, in all probability, from year to year, although our studies are not extensive enough to determine this point.

The seasonal distribution is different for different members of the plancton. Some types are perennial and others strictly seasonal in occurrence. The former include Dinobryon, Diaptomus,[27] Cyclops, Anuraea and Notholca. Nauplii, as would be expected from the occurrence of the parent forms, are perennial, while Ceratium, Difflugia, Asplanchna, Gastropus, Polyarthra, Daphnia, Bosmina and several others are seasonal.

Most zoöplanctonts have their maximum in June. Ceratium, Difflugia and Gastropus are, however, exceptions, their maximum occurring in September-October. Daphnia and Bosmina are so uncommon at all seasons that it is difficult to assign them any definite maximum. They have two seasons, however, June-July and October and are very rare or absent in winter and spring. Polyarthra also is a warm weather form, being very rare when the temperature of the water is near 4.°

The maximum of Ceratium in Flathead Lake occurs considerably later than is usual, it being ordinarily a typical summer form, although it is not limited to this season. Thus in the Greifensee (Guyer, 1911) it has two maxima, a major one in July and another minor one in December, while a

* See page 124.

[27] Very rare during the autumn.

similar seasonal distribution is found in many Swiss lakes, according to this author.

Peridinium is rare, being seldom found in the plancton in 1928. In 1929 it had a maximum between April 16 and June 16, reaching a peak of 600 pr. l. at 18 m. depth on June 1. From June 27 to February 3, 1930 it was very rare, though usually present in a few collections of each series.

Mallomonas is still more rare than Peridinium. Curiously enough its maximum period was in August 1928 with a peak of 500 pr. l. at 12 m. on August 9. It occurred in a few collections of each series from April 16 to June 1, 1929 and thereafter was rarely seen. This seasonal distribution is very different from that in the Lake of the Four Cantons where, according to Bachmann (1911) Mallomonas has its maximum in winter. In the latter lake, however, the species (*producta* and *acaroides*) are different from that (*caudata*) in Flathead Lake, which may, possibly, explain the difference in seasonal maxima.

Actinophrys sol occurred sparingly in the plancton from August to December with a maximum of 300 pr. l. at 12 m. on August 30, 1929.

Other protozoans occasionally encountered in the plancton are *Arcella vulgaris, Centropyxis aculeata, Cyphoderia ampulla, Euglypha alveolata, Vampyrella lateritia* and Anisonema.

The succession of some forms is very striking. It is as if one organism held sway for a brief period and then stepped aside to make way for another. This is particularly noticeable in the distribution of Ceratium and Difflugia, and Asplanchna and Gastropus. From June 1 to November 28, 1929 Ceratium was present in scattering numbers during June and July, increasing in abundance in August, and in large numbers in September-October. In November it fell off rapidly in numbers and was very rare in winter. Difflugia, on the other hand, was present in small numbers from February to May, reappearing in September and continuing till February 1930, with a rather well marked maximum in December. Asplanchna was present from February to July 1929, while Gastropus appeared in very small numbers in the July 12 collection and continued until February 1930, with a rather poorly marked maximum in early September. The reasons for these successions is undoubtedly to be sought in the general environment rather than in any close interrelation between the forms concerned.

The seasonal distribution of the nauplii closely parallels that of the parent forms, Cyclops and Diaptomus; their number, however, averages somewhat greater than that of the parents, indicating a high immature death rate.

The sex ratio of certain forms shows marked seasonal variations. On April 16, 1929 the ratio for Cyclops was 67♀s to 7♂s. This proportion of approximately 10:1 gradually increased, with an exceptional drop of 10:6 on August 9, until September when the ♂s had nearly disappeared. On October

26, however, the ratio was 76:5 and continued at approximately 80:3 until the completion of the plancton work on February 3, 1930.

In Diaptomus the number of ♀s far outranks that of the ♂s during most of the year, but in late autumn and early winter the proportion of the sexes is more nearly equal. In mid-July 1928 the ratio of the sexes was 159♀s to 7♂s on the 11th and 30♀s to 5♂s on the 19th. On the 26th ♂s were not noted and were absent in the counts from then on to September 28 when one was noted. Meantime the number of ♀s had also diminished very greatly, ranging from 3 to 0 pr. l. from August 30 to November 3. On the latter date the ratio of ♀s to ♂s was 2:1. By February 23, 1929 the ratio had risen to 7:1. During June and July there was a slow and irregular increase in the ratio until August 30 when males were absent in the counts, and remained so until late November with the exception of a single individual on October 26. On November 28, however, ♂s were present in considerable numbers, the ratio of ♀s to ♂s falling to 13:9½ on the latter date, but rising again to 12:2½ on February 3, 1930 when the collections ceased.

These ratios indicate that during most of the year reproduction in the copepods is preponderantly parthenogenetic and about exclusively so in late summer and early autumn. During the colder seasons of the year and extending from spring into mid-summer, bi-sexual reproduction occurs to some extent, but even then parthenogenesis is probably the chief method. Birge (*l.c.*, p. 340) has observed that in Lake Mendota Daphnia hyalina has almost completely lost the capacity for sexual reproduction, "males never exceeding 4% of the number of females and rarely being as numerous as this." In our collections this species, which forms the major part of the Cladocera, has a distinct period of sexual reproduction in the autumn, the males averaging about 20% to 80% of females at this season.

Our results for both Copepods and Cladocera in respect to the sex ratio, agree quite closely with those of Kühl (*l.c.*) for the Walchensee in Bavaria.

In respect to reproductive cycles of the Cladocera, Flathead Lake resembles those alpine lakes in which, according to Wesenberg-Lund (1908), reproduction is di-cyclic, while Lake Mendota resembles the sub-alpine and Baltic lakes in which "there is a decided tendency to a-cycly" (*l.c.*, p. 316).

The vertical distribution of the various planctonts, collectively and individually, is very irregular, all of the distribution curves having a zigzag form (Figs. 6-9.) This type of curve is conspicuous in all diagrams of vertical distribution and is probably due to inequality in horizontal distribution in spite of the generally held opinion to the contrary, as pointed out elsewhere in this paper.*

Naturally no two organisms have exactly the same vertical distribution,

* See page 126.

nor is the distribution of any species necessarily the same at different seasons or even at closely approximate dates, which latter fact may also be due in part at least to variations in horizontal distribution already discussed.

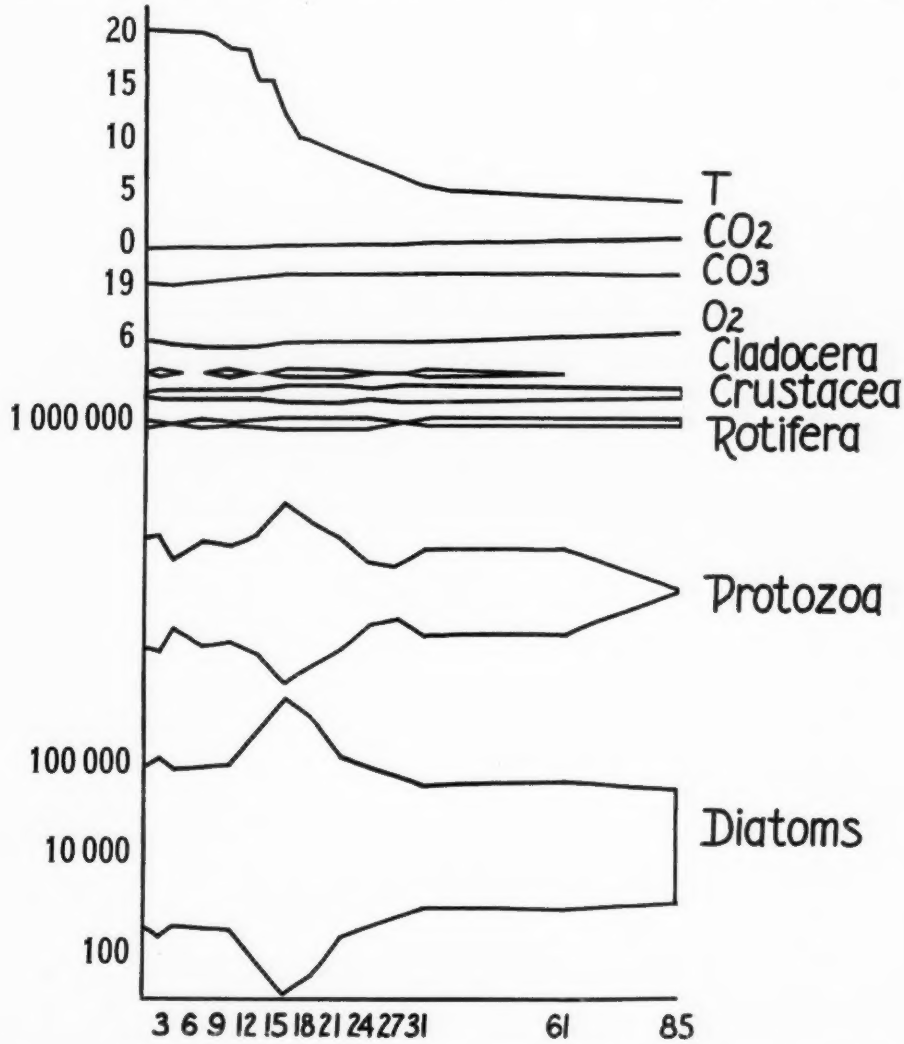

FIG. 6. Vertical distribution of plancton, temperature, and dissolved gases at Station 1, August 18, 1928. Temperatures and gases are plotted to an arithmetic, plancton to a spherical scale (i.e., as the cube root of the number of organisms). Vertical scales for all variables are shown on the chart, temperatures in degrees centigrade, gases in cc. pr. 1. Depths are shown to the nearest meter, the scale below 31 m. being one half that above 31 m.

The vertical distribution of the various phytoplanctonts is, in general, similar. During winter and spring the distribution from top to bottom is approximately equal, but, with rising temperature and increasing light in June, they recede from the surface and present a maximum somewhere between 15 and 30 m. Most of the zoöplanctonts have a more or less similar type of distribution, with a low point near the surface, a maximum some-

where above the 30 m. mark and a rather sharp decrease in this region with small numbers from there to the bottom. The absence of samples between 31 and 61 m. in most of our collections probably does not invalidate this general conclusion, since in those collections which do have samples from intermediate depths, the same general results are found. A secondary maximum may, however, occur below 31 m. and in one case (nauplii—8/9/28) the maximum occurred at 49 m.

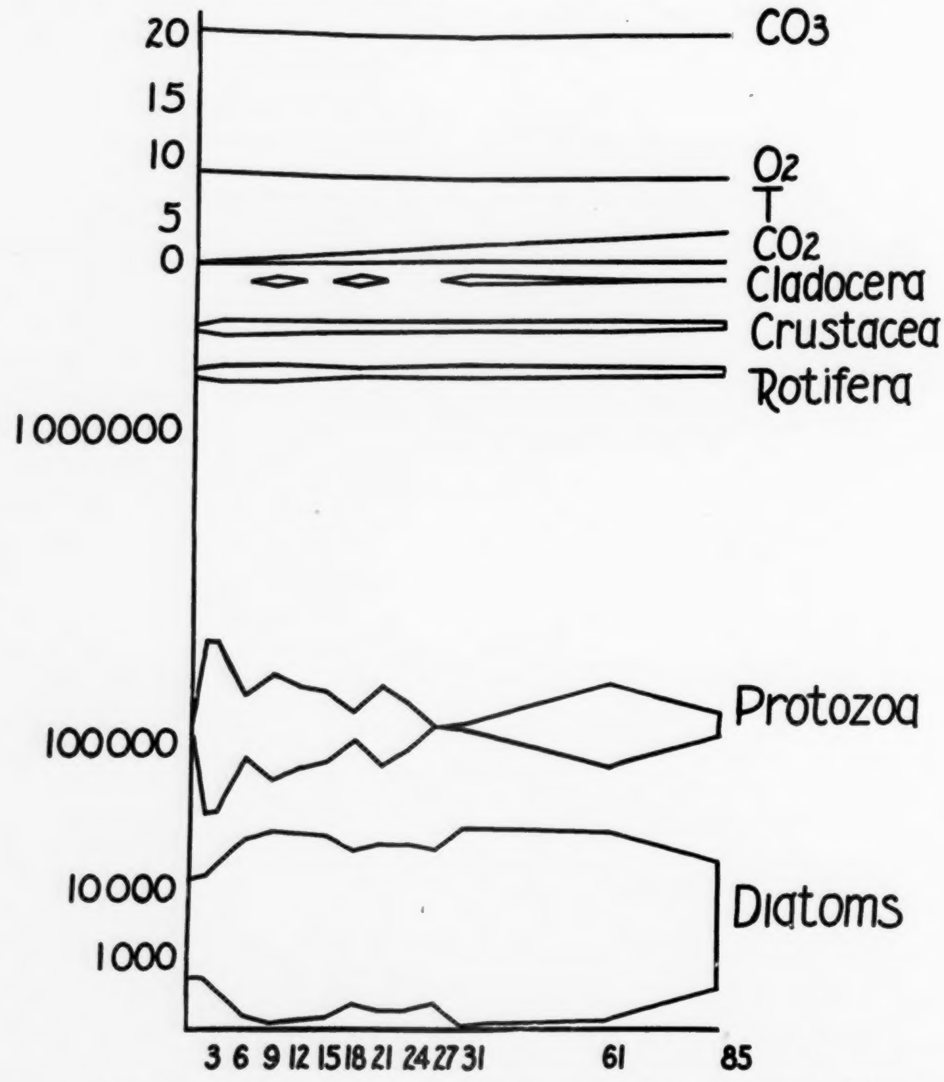

FIG. 7. Vertical distribution of plancton, temperature and gases at Station 1, February 23, 1929. For description see Fig. 6.

While most zoöplanctonts have their maximum between 10 and 30 m. and thus within the limits of the thermocline, with relatively small numbers in the upper levels, Ceratium has its maximum always in the upper 20 and usually in the upper 15 m., and is frequently present in large numbers near

the surface. Dinobyon also is occasionally abundant at the surface. Difflugia, on the contrary, while scarce at all levels, is usually more numerous below 15 m.

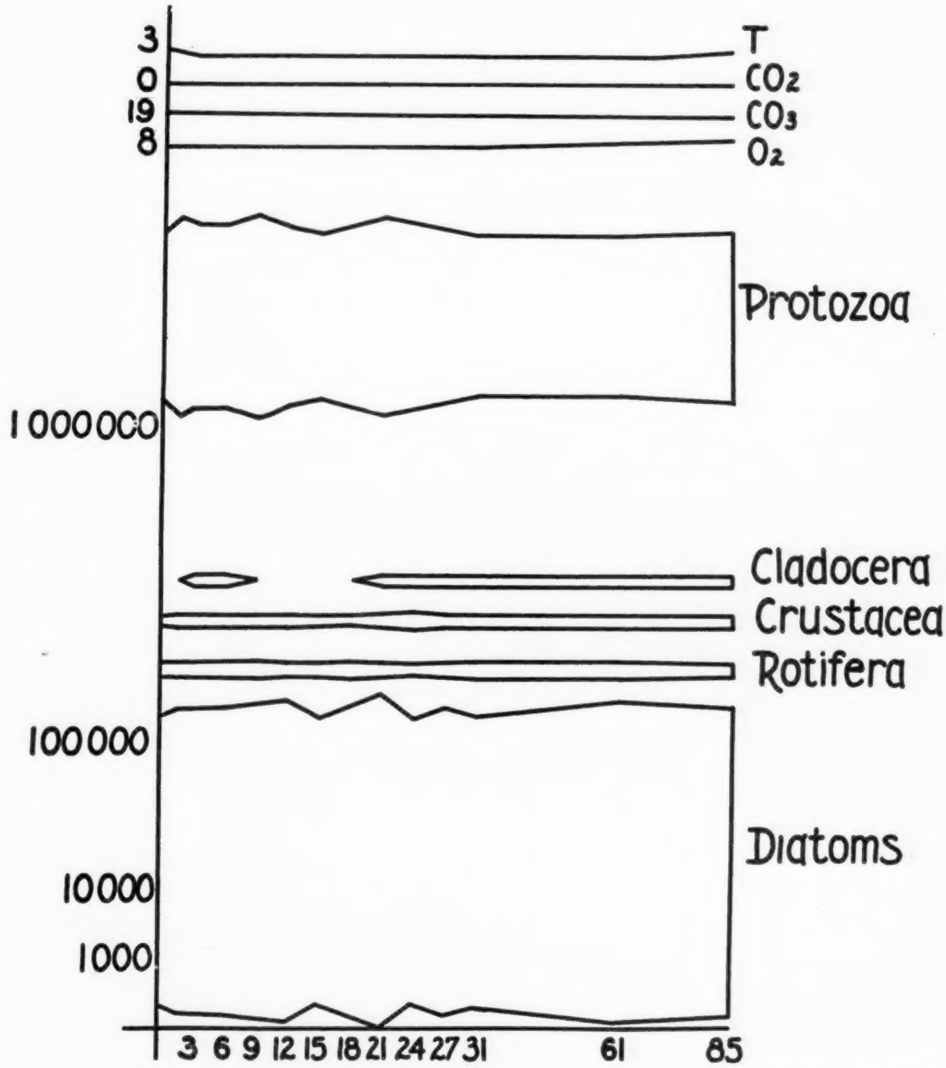

FIG. 8. Vertical distribution of plancton, temperature and gases at Station 1, April 27, 1929. For description see Fig. 6.

When the temperature of the lake approximates 4°, however, the distribution curve of most species straightens out, that is, the species becomes more uniform in distribution from top to bottom, or may even increase conspicuously in the lower levels, as was the case on April 16, 1929 where each species charted had its maximum at some point below 30 m. Anuraea, however, presents a rather marked exception to the rule of more uniform distribution in the colder water, for in February of both years (1929-30) it had a distinct maximum at 6 m. By April, 1929, however, it had moved down-

ward, at which time its distribution conformed more nearly to that of the other zoöplanctonts.

While all of the distribution curves show marked irregularity, there is generally more or less of a gradual approach to, and recession from the maxima and minima. The numbers do not ordinarily jump from zero to

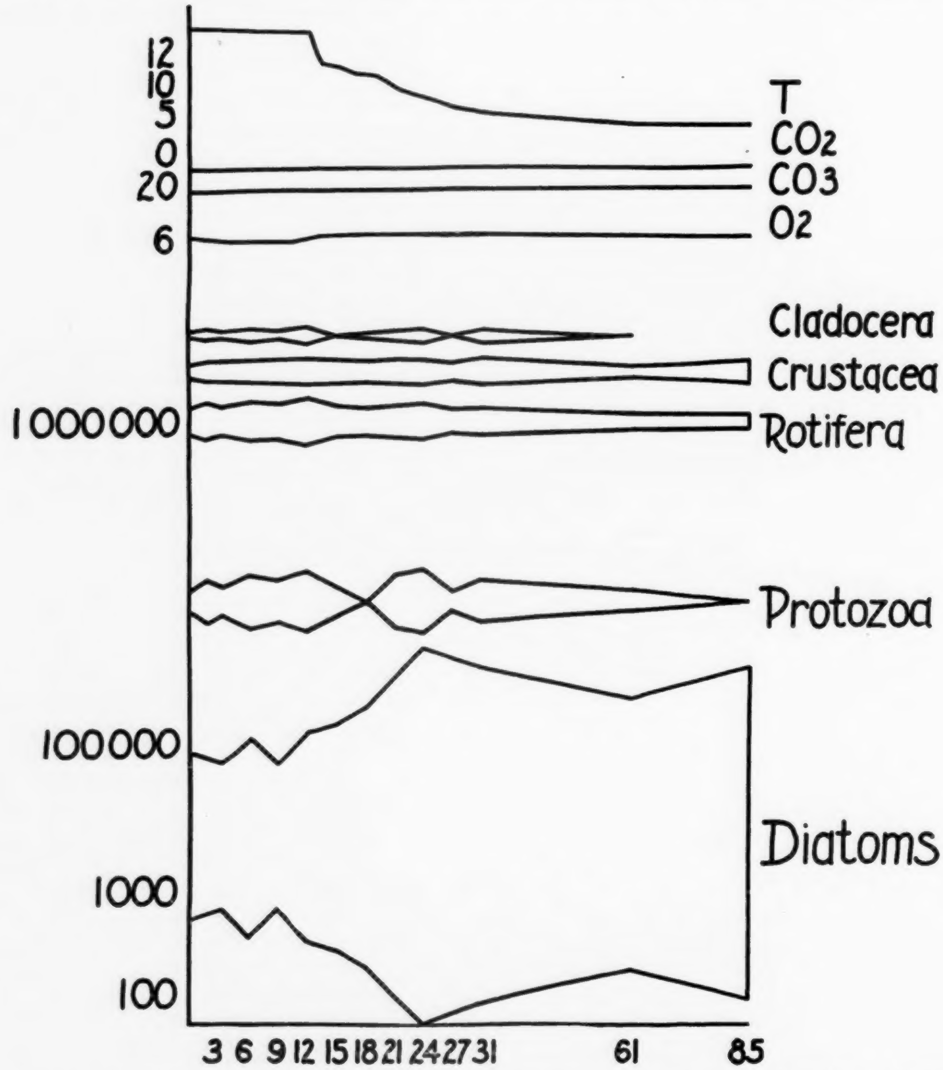

FIG. 9. Vertical distribution of plancton, temperature and gases at Station 1, June 16, 1929. For description see Fig. 6.

the maximum or vice versa in a 3 m. interval. But this happened in the case of Gastropus on August 9, 1928 when this species, which was absent in the upper 10 m., suddenly appeared in the amount of 51 pr. 1. at 12 m., decreasing rapidly from here to 21 m. and disappearing about the 24 m. level.

Birge (1897) and Birge and Juday (1914) have called attention to two types of vertical distribution with respect to the thermocline. In one type

the zoöplancton is scarce in the hypolimnion and in the other is present there in considerable quantities. The former type of distribution may be due either to scarcity of oxygen or of food in the hypolimnion, while the latter type is due to an ample supply of both in this layer. According to Birge and Juday (*l.c.,* p. 588) the "chlorophyl-bearing portion of the plancton" is "confined chiefly to the epilimnion, where light conditions are most favorable", but in cold, clear, deep mountain lakes (*i.e.* Crater Lake, Oregon, and Lake Tahoe, California, Kemmerer et al., 1923) the maximum amount of phytoplancton may occur well below the thermocline. Apparently light rather than temperature is the controlling factor here.

A similar conclusion is drawn for the Walchen and Kochel lakes by Kühl (*l.c.*), who ascribes the vertical distribution of the plancton in these lakes primarily to the influence of light, while "Ein Einfluss der Sp-Sch. auf Verteilung besteht nicht" (p. 155).

Our own observations support this view, for in Flathead Lake the zone of maximum plancton development is at the lower limit of, or well below the thermocline.

According to Birge and Juday (*l.c.*) the food supply of the zoöplancton (*i.e.* the amount of chlorophyllaceous organisms) present in the hypolimnion depends directly on the amount produced in the epilimnion and inversely on the amount consumed by the zoöplancton there present.

In Flathead Lake the vertical distribution of the zoöplancton is intermediate between these two types. While the population of the hypolimnion is in general much less numerous than that of the epilimnion and the thermocline, it always contains a considerable number of planctonts. The vertical distribution of the plancton is clearly a resultant of three factors, food, light and temperature.

Hofer (1899) in a study of several mountain lakes of Austria and Germany maintains the existence of an abyssal lifeless region in all deep lakes. But this is denied by Kühl (*l.c.*), who has shown an increase in the number of copepods at certain times in the 175-190 m. level in the Walchen Lake, which has a maximum depth of 192 m. It is refuted also by the distribution of life in Lakes Baikal and Tanganyika (Thienemann 1925).

Birge (*l.c.*) finds the young Crustacea nearer the surface than the older ones. While we have not made a careful study of this question, our observations differ from those of Birge. In general the larval copepods (both nauplii and later stages) average deeper in their distribution than do the older stages, while there is no evident difference in the distribution of the young and adult Cladocera. As Naber (1933, p. 96) points out there is no constant relationship in this regard.

Our collections at stations other than No. 1 are too few to enable me to draw any very definite conclusions regarding the horizontal distribution

of the plancton in Flathead Lake. A priori it was expected that the shallow bays (Stations 2, 3, 8, 9, 10) would show much higher results than the open lake, because shallow waters are, in general, more productive of plancton than are deeper ones, and because of the higher aquatic vegetation which is more or less abundant in the bays. It should be borne in mind, however, that the quantitative collections were necessarily made outside, though in rather close proximity to the areas of dense vegetation; and, consequently, the amount of life within the latter is not shown. In general, however, our expectation has not been realized. In some cases the shallow water collections show much higher results than do those from deeper water, especially among the rotifers and diatoms, but the results are by no means consistent. Station 8, for example, at the mouth of the Swan River, gives results which are generally low as compared with those at Station 1 in the open lake, with the exception of Dinobryon, which in three of the five collections was higher, and in two lower in number than at Station 1 on the approximate dates. Asterionella also is exceptional, for it reached a peak of 404,000 cells pr. l. at 1.5 m. depth on July 2, 1929, while at Station 1 on June 27 its maximum was 65,000 pr. l. at 30 m., and on July 12, 43,000 at 27 m.

The comparative results show clearly the inequalities which may exist at different stations at corresponding times. Thus, on July 4-5, 1929 there were great numbers of Anuraea and Notholca present at the southern and western ends of the lake (between Hell-Roaring Bay and Dayton), while on July 2, 1929 at the northern end of the lake (Somers) the numbers were much smaller.[28] At the mouth of a tiny creek near Dayton on July 4, 1929 the relatively enormous number of 296 Bosmina pr. l. were present in the surface water, while this genus has never numbered more than 13 pr. l. in any sample from any other point, with the exception of Station 10 (near Elmo); where, on this same date, it numbered 50 pr. l. at the surface. Several other instances of the same sort could be cited, but these are, perhaps, the most striking cases, and serve to illustrate well the usual inequality in distribution at various points. Here, of course, we are dealing with distribution in somewhat different environments. Regarding inequalities of distribution in the same environment see page 125 *et seq.*

Reparding the relative abundance of plancton at the periphery and the center of a lake differences of opinion exist. Thus Linder (1904) believes that the latter is the more populous area, but this opinion has not been supported by Guyer (*l.c.*), and in my own work (Young, 1924) I was unable to find any consistent differences in amount of plancton at the shore and at some distance therefrom.

[28] At Station 2 in Hell-Roaring Bay on July 5, 1929, Notholca averaged 381 pr. l.; at Station 3, Somers, on July 2, 1929, 18 pr. l.; while for the same places and dates Anurea averaged 332 and 11 pr. l. respectively.

THE LITTORAL AREA

As already stated,* in the littoral area may be included all of the shore area to a depth rather arbitrarily taken at 10 m. Most of this region consists of rocky, wave-beaten shores with a rather distinct drop-off. A little of the shore has gravel beaches, while at the northern end of the lake the Flathead River delta has formed a rather extensive sandy shore.

Submerged rocks and logs near the shore are covered with a slimy growth of stalked diatoms (Gomphonema, Cymbella) and filamentous green algae (Bulbochaetae, Oedogonium, etc.).

The principal animal inhabtants of the rocky shores are insect larvae and molluscs. The former are chiefly Ephemerida and Trichoptera with occasional Plecoptera; and the latter Lymnea, Physa, Planorbis and Valvata, of which the first is the most numerous.

Capsules of the leech (*Herpobdella punctata*) are found commonly on the rocky shores, mainly at depths less than a metre, while animals of occasional occurrence are Hydra, Fredericella, Spongilla, Gammarus, Chironomids, annelids, planarians and a host of species including Protozoa, rotifers, copepods, cladocerans, etc., many of which are doubtless adventitious, being carried in from the open lake by currents.

The sandy beaches near the Flathead River inlet have not been very thoroughly studied. Lacking any protection from the heavy surf to which they are often exposed, they appear to have no macroscopic life whatever.

THE BAYS

I have already made some comparison between the life of the bays and that of the open lake.* The collections on which this comparison was based were necessarily, however, made in open water and revealed nothing of the life which inhabits the shore line and the plant societies (Scirpus, Potamogeton, etc.) In these habitats, especially the latter, occur all the lake inhabitants with the exception of some of the fishes, while fully 90% of them are restricted to these habitats.

The bays differ widely in character. Many, such as Woods and Yellow bays, are essentially nothing more than deeper or shallower indentations in the general shore line, and, aside from providing protection from wind and a settling place for water-logged forest debris, afford a habitat similar to that of the open lake. Others, of which Hell-Roaring Bay is the most striking example, are shallow, with gently sloping muddy bottoms, which support a luxuriant growth of various aquatic plants. The former differ but little in their biotas from the open lake, but the latter support a large assemblage of forms, most of which seldom occur in deep water, while many are never found there. The bottom of the shallow bays is submerged at high water in

* See page 117.
* See page 136.

early summer, but with the recession of the lake in late summer and fall, extensive areas are exposed. These bays offer a suitable habitat for the various species of aquatic seed plants which occur in the lake, most common of which are the following: "*Scripus validus, Batrachium trichophyllum, Polygonum amphibium, Sagittaria cristata, Eleocharis palustris, Acorus calamus, Hippurus vulgaris, Myriophyllum verticillatum, Typha latifolia, Potamogeton natans, P. pectinatus, P. perfoliatus, P. filiformis, P. compressus,* and *P. heterophyllum.* In addition to these aquatic seed plants the scouring rush (Equisetum) is found in the same regions.

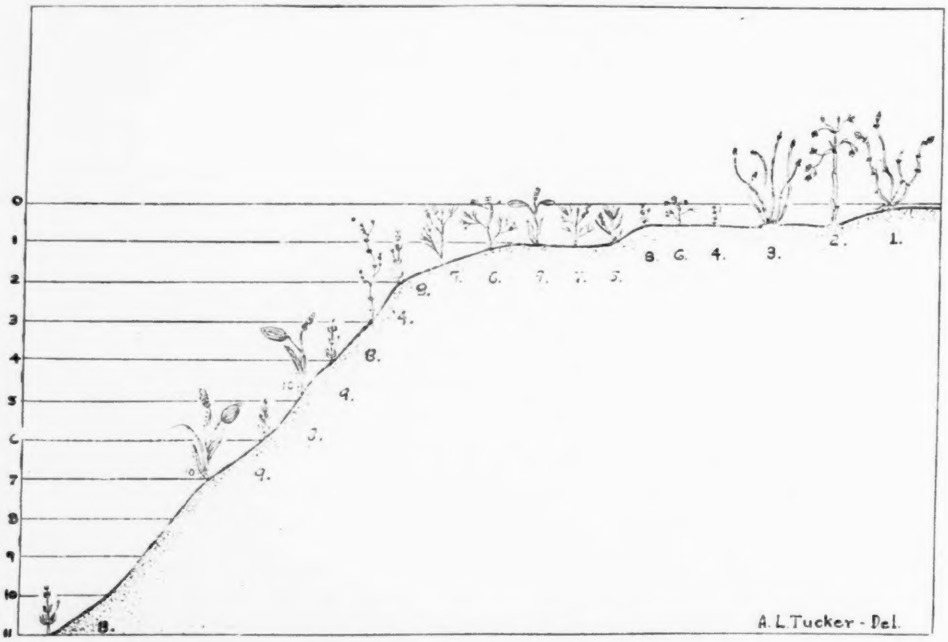

FIG. 10. Distribution of the larger aquatic vegetation on the lake shore. The steepness of slope of the lake bottom is necessarily much exaggerated.

1. Equisetum sp.
2. Scirpus validus
3. Eleocharis palustris
4. Myriophyllum verticillatum
5. Potamogeton compressus
6. Batrachium trichophyllum
7. Potamogeton pectinatus
8. Chara sp.
9. Potamogeton natans
10. Attached forms of various algae

Such plants as these crowd the shore line but rapidly diminish in numbers in deepening water. They grow more numerously at the edge of the water because of abundance of air, moisture and light, while a few can grow wholly submerged. None of them can endure the beating of the waves on exposed shores such as are so prevalent in this lake. Thus it is that the scarcity of sheltered bays acts as the limiting factor to the number of the higher aquatic plants found in Flathead Lake. As a concrete illustration of the distribution of such aquatics along the shore line, the following diagram (Fig. 10) will serve to show the association of such plants. This diagram, though illustrating the life zones of the higher plants at Big Fork, is typical of the other bays in the lake to a greater or lesser degree.

The low flats exposed at low water are covered with species of Equisetum, Scirpus, Eleocharis and Typha. These plants while able to grow in standing water are never completely submerged. Among the submerged plants are Batrachium, Myriophyllum and Potamogeton. In addition to those mentioned the Stone-Wort (*Chara sp.*) is found in large numbers in the shallow portions of the lake growing attached to the bottom. It is usually incrusted with lime and although seldom eaten by any of the aquatic animals, it forms a shelter for them as well as a means of attachment for many forms of lower plants."[29] The stems of plants and submerged sticks and logs offer convenient attachments for numbers of filamentous algae (Cladophora, Spirogyra, Ulothrix, etc.), while floating in the sheltered waters are to be found all of the pelagic forms and a host of others.

"The numbers of these minute plant forms can be better appreciated when it is stated that fifty-one species of algae were found and identified from one collection made at Big Fork on July 5, 1929. This does not include the many species of diatoms that have not yet been identified. The same could be said for Hell-Roaring Bay for it was there that probably over one-half of the algae were collected."[29]

THE BOTTOM FAUNA

As in the case of the pelagic inhabitants of the lake, so too in that of the bottom dwellers it is difficult or impossible to draw any line between littoral species and those inhabiting the deeper water. In both cases the presence or absence of vegetation is one of the factors in limiting the distribution of littoral life. With the bottom fauna the character of the bottom and the presence of suitable hold-fasts and shelters in the form of rocks or logs are important factors in determining the distribution of species in addition to those of pressure, temperature, etc.

Our study of the bottom organisms of Flathead Lake has not been complete, but a fairly careful study of the bottom fauna has been made in Yellow Bay and the adjoining lake, for comparison with the character and amount of this life with that in lakes elsewhere. Our collections include five series for quantitative study taken in September, 1930 and March, May, July, August and September, 1932, from a depth of 1.5 m. in Yellow Bay to one of 94 m. in the open lake about 2 km. from shore, together with a few qualitative collections at several widely separated points in the lake.

The results of these collections are given in Table 10 and Figures 11-12, which show the distribution of the bottom life at various depths between Yellow Bay and Station 1 in the open lake at different times.

The bottom deposits have already been discussed,* and this discussion is presupposed in what follows here.

In the case of the inhabitants of such vegetation-rich areas as a part of

[29] Ms. notes of C. W. Waters.
* See page 97.

Hell-Roaring Bay and Big Arm near Dayton, it is difficult to tell which animals live both on the bottom and on the vegetation, and which are confined to the bottom only. We have found that those samples containing plant material give consistently higher counts than do those in which this is lacking.

TABLE 10. Distribution of bottom life in Flathead Lake at different depths and seasons.

9-4—9/8/30	Turbellaria	Nematoda [30]	Mermithidae	Oligochaeta	Hirudinea	Amphipoda	Hydracarina	Ephemerida	Trichoptera	Odonata	Coleoptera	Chironomidae	Sphaeridae	Gastropoda
9 m.				96			64	16				112	80	
15 m.				48			16					224		
23 m.	16			80			32					96	16	
35 m.												16		
49 m.												64		
89 m.												16		
AVERAGE [31]	3			37			28	16				88	16	
3/14/32														
10 m.	16			112		672	16	16–32 [32]	16	32		2736	288	48
14–17 m.				40	16		16					768	56	
32 m.		16										224	16	
AVERAGE [31]	4	4		48	10	672	12	16–32 [32]	16	32		1124	104	16
5/12–15/32														
Sand 3 m.												48	48+ [33]	48+ [33]
9 m.				32+32 [33]		48	80	16				1536	16	
17 m.				48+16 [33]	16							304+32 [33]	16	32
35 m.				[32–33]			16					64		
AVERAGE [31]				20+ [33]	5	24	24	8				488	20	27
7–8/32														
1–1.5 m.					8							40	56	
6–9 m.				40	16	40	8		60	8		276	180	52
18–24.5 m.		40	8	40								112	24	
30 m.												368		
55 m.	16	160	32									128		
83–91 m.		496		16								48	8	
AVERAGE [31]	2	103	4	16	12	20	23		30	4		147	64	26
8–9/32														
1.5 m.	8					152		32	8	24	32	48	56	104
9.5 m.	16 [32]				16	32						112		
31 m.		48+16 [33]	16									288		
94 m.		1456	64	80								112		
AVERAGE [31]	8 [32]	376	20	20	8	92		16	4	12	32	140	14	52

[30] The numbers of nemas recorded in Flathead Lake are probably much too low, due to the difficulty of finding the minute organisms in the very fine ooze which covers the lake bottom, and in the earlier collections (prior to July, 1932) they were probably overlooked altogether.

[31] Averages based on number of collections down to, and including only the maximum depths at which each group occurs. Of the above groups the following are apparently restricted in distribution to the depths specified: Turbellaria, 55m., Hirudinea, 17m., Amphipoda, 10m., Hydracarina, 35m., Ephemerida, Trichoptera and Odonata, 10m., Gastropoda, 17m.

[32] Record uncertain.

[33] Fragments.

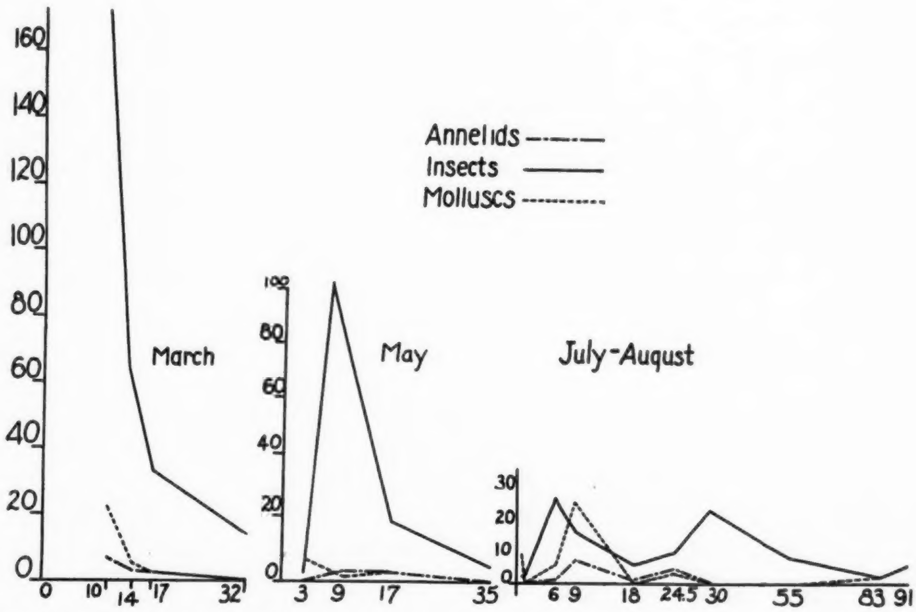

FIG. 11. Depth distribution of the bottom fauna in different months. Numbers pr. sq. m. plotted as ordinates, dates as abscissae.

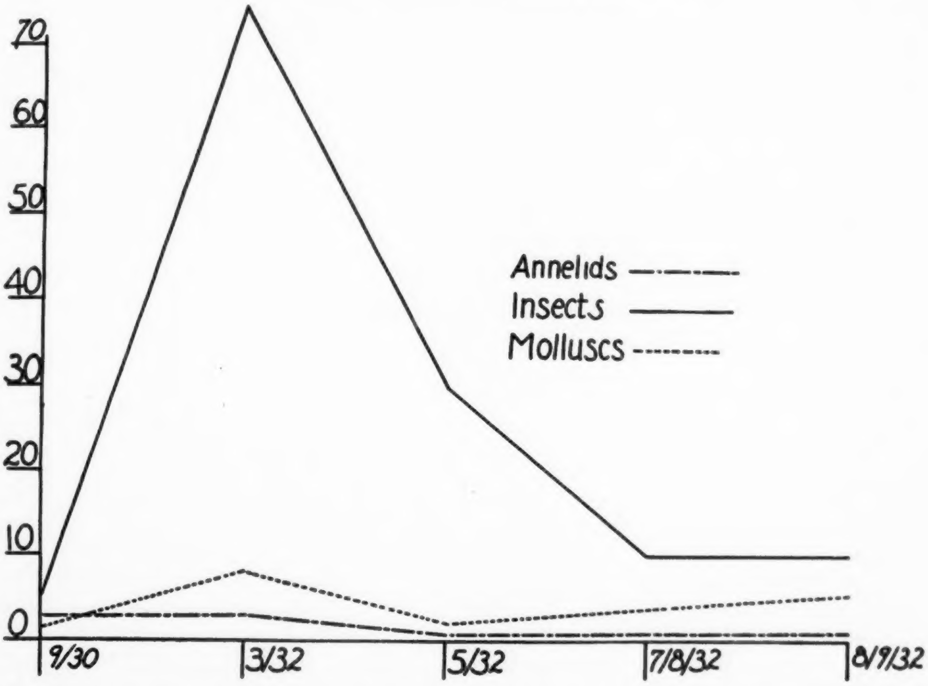

FIG. 12. Seasonal distribution of the bottom fauna. Vertical scale = number of animals pr. sq. m. The dates are given as abscissae.

In order to make a comparison between the number and kinds of animals present on the bottom, which is barren of plants, and on that which is plant covered, we have taken samples in closely adjacent areas, one covered with

Myriophyllum and the other free therefrom. Both were areas of sandy bottom at approximately equal depths (1.5 m.). The results, which are given in Table 11, show clearly the greater abundance of animals among the plants than on the comparatively plant-free areas. Dredging a mass of Chara from Yellow Bay at a depth of 8-10 m. yielded in an incomplete count 27 chironomids, 2 leeches, 1 Gammarus and 2 molluscs. From these results, incomplete though they be, it is very evident that much of the material taken in the dredge comes from the higher plants growing on the bottom, which fact must be taken into account in any study of depth distribution of animals. Even more striking is the comparison of Lundbeck (1926, p. 118) in which he gives a total of 6,622 animals pr. sq. m. at a depth of 0.5 m. on a sandy bottom covered with Chara, and 633 on a similar bottom, partly stony and without Chara.

TABLE 11. Numbers of bottom animals pr. sq. m. in two closely adjacent areas.

	In Myriophyllum	On open bottom
Hydra	64	
Hyalella	304	16
Acarina	16	
Ephemera	16	48
Trichoptera (cases)	80	16
Coleoptera	64	
Enallagma	48	
Chironomidae	32	4
Helisoma	16	
Gyraulis	112	
Valvata	64 (and one empty shell)	16
Pisidium	64 (sev. empty shells)	48 (sev. empty shells)
Total	880	192

Thienemann (1926, p. 51) says . . . "die Besiedelung des Bodens eine flachenhafte sein muss; auch der weiche Schlamm ist nur in seiner Oberfläche belebt, schon in einer Tiefe von ein paar Zentimetern hört alles Leben auf", while, according to Lundbeck (1926, p. 80) the "Bodentiere (with exception of the Tubificidae) auf die Schlamm-oberfläche beschränkt sind."

I have made a few tests to determine the accuracy of Thienemann's view by sinking a tube into the bottom and examining different depths of the core extracted by it, by collecting with a hand scoop in shallow water samples of bottom deposits from the surface and below it, and by examining samples taken with the Eckman dredge, in which the surface ooze could be readily distinguished by color from the deeper layers. These tests indicate that most of the bottom forms live in the surface layer or a very few centimetres below it. But Dorylaimus, of which vast numbers occupy the deep bottom of the lake, appears to be more abundant at a depth of 4-12 cm. in the ooze than it is above this level in the deeper parts of the lake. In such a situation their only apparent means of nutrition is by osmosis from the ooze, and of what use the spear,

which is a characteristic feature of this genus, can be, is problematical. It seems likely that they are adapting themselves to a new habitat, and that, in course of time, the spear may cease to function and degenerate, as seems to be the case with the intestine of the mermithids. Why these worms are so abundant in the deeper parts of the lake and relatively uncommon in the shallower waters is also an unsolved problem.

Omitting the sub-microscopic forms such as ostracods, cladocerans, etc., our collections show a total of at least 38 benthic animals in Flathead Lake, while a record by Forbes (1891) of Plumatella brings this number to 39. Were specific determinations possible for all of the chironomids, annelids and Trichoptera, the list would be much increased.

Of this assemblage the Chironomidae are evidently the commonest forms, with Chironomus at the head of the list. Next to the chironomids the oligochaetes and sphaerids are most numerous. The chironomids include the genera Chironomus, Tanypus, Tanytarsus, Corynoneura, Orthocladius, Bezzia and Ablabesmyia. Hyalella, which is frequently common in bottom collections, probably owes its abundance to the presence of vegetation there.

According to the classifications of Thienemann (1923) and Naumann (1927), oligotrophic lakes, to which class Flathead Lake belongs, have a Tanytarsus fauna and lack Corethra, while the eutrophic and dystrophic lakes have a Chironomus fauna and the presence of Corethra. In Flathead Lake Tanytarsus, while present in considerable numbers, is by no means the dominant midge, being outnumbered probably 2:1 by Chironomus. The absence of Corethra, however, is a striking feature of the insect fauna of the lake.

The vertical distribution shows a marked decrease in number of organisms with increase in depth. Between 25 and 35 m. bottom life mostly disappears with the exception of chironomids and nemas, an occasional annelid, planarian and, possibly, a few microscopic organisms. Thus, the bottom fauna corresponds rather closely in its depth distribution with the plancton, which, as already shown,* is generally much less abundant below than above 35 m. The factors determining the distribution of the former are probably temperature, pressure, possibly light and food and, in the case of some, shelter and hold-fasts. Lack of bottom oxygen, which undoubtedly influences the benthos in lakes of the eu- and dystrophic types, can play no part here at any season.

In Shakespeare Island Lake, Ontario, Cronk (1932) found the profundal zone (below 6 m.) "poor in species, but rich in numbers" (*l.c.*, p. 56). In Flathead Lake the same type of distribution occurs, but the "profundal" zone lies at a much greater depth, and is characterized chiefly by the nematode

* See page 132.

Dorylaimus. In Lake Nipigon on the contrary (Adamstone, 1924) the average number of bottom animals does not differ greatly at any depth.

Eggleton (1931) and Lundbeck (1926) have shown that in some lakes differences in depth distribution of benthic animals occur seasonally, the concentration zone moving deeper in winter and rising in summer. We have not observed this change in the concentration zone in Flathead Lake, but our observations are rather too limited to admit of any certain conclusions on this point.

In the Japanese lakes studied by Myadi (1931, 1932) "A comparison of the bottom fauna at different seasons of the year shows remarkable changes in the distribution of some animals and none for others. Examples of the former are larvae of some Chironomidae and of Corethra" (1931, p. 223). In the case of Corethra the young larvae settle in shallow bottoms in summer, migrating into deeper water as they become older. The reason for this is still doubtful. Myadi suggests that negative phototropism may play a part. The larvae of Endochironomus, on the contrary tend to move upward from deeper levels as the oxygen decreases therein.

Eggleton (*l.c.*) and Juday (1922) have shown a very marked seasonal periodicity of Corethra, the maximum numbers occurring in March and the minimum in August. Our observations confirm these results by showing a greater abundance of insects in the benthos in March than in May or September (Fig. 11). This difference is readily intelligible as cyclic in character, but how many broods occur every year we do not know. Muttkowski (*l.c.*, 1918) believes that there are at least three of Corethra in Lake Mendota. Lundbeck (*l.c.*, 1926), on the contrary, finds that in the lakes of northern Germany most species of bottom organisms reach their maximum in early autumn. According to this author, Chironomus bathophilus, one of the most abundant midges, has a single swarming period (May), while another common midge (C. plumosus) swarms from June to November.

Myadi (*l.c.*, p. 99) also says that "in oligotrophic lakes the population is greater in October than in July."

GENERAL DISCUSSION

An ecological study of any area, whether land or water, is of both local and general interest; of interest not only in determining the relation which exists between the members of the local community of organisms which it harbors and their environment; but also in comparing this relation with those in similar communities elsewhere, in the attempt to classify all of these communities, and to discover the general laws underlying such classification.

The ecological classification of any area must be based upon all factors—physical, chemical and biological. Thienemann (1925) has made a valuable contribution to the classification of inland waters, and I shall follow his scheme in my attempt to compare Flathead Lake with those elsewhere.

According to Thienemann, fresh water lakes may be divided into oligotrophic, eutrophic and dystrophic types. Flathead Lake clearly belongs to the first of these types which includes mountain lakes in general and is characterized by:

1. Considerable size and depth.
2. High purity.
3. Low turbidity and, vice versa, high transparency.
4. A low average temperature for the whole body of water.
5. A distinct thermocline in summer.
6. Ample oxygen at all depths.
7. A bottom temperature varying but little throughout the year.
8. A comparative poverty of plancton which is distributed mainly in the upper fourth or third of the lake.

There are many other characteristics of this type of lake but the above will amply suffice to define it.

The plancton productivity of a lake is a question of both ecological and economic interest, expressing on the one hand the ecological factors in terms of amount of life, and, on the other, determining in large degree the variety and abundance of fish, which are, after all, the final expression of the lake's fitness as a home for living things.

Table 12 shows the number of organisms pr. 1.[36] for 12 North American and one European lake compared with Flathead Lake. In compiling the table, I have selected those data which are, as nearly as possible, comparable in respect to season, although the variability in plancton abundance from season to season, and even from day to day, is so great as to render such a comparison at best only approximate. In comparing these data, furthermore, the difference in methods of collecting must be borne in mind,* as well as the small number of collections available from many lakes of similar character elsewhere.

In "Lakes of the Northwestern United States" (Kemmerer et al, *l.c.*) the authors have collected data on fifty-two lakes in Idaho, Oregon, Washington and California, showing the physical and biological conditions in these lakes with reference to fish culture therein. These lakes range from those two or three hectares in area to Lake Pend Oreille with an area of 322 sq. km.; and in depth from those of 2 m. to Crater Lake, Oregon, 610 m. deep, "the deepest known lake in the United States".

I have selected four of these (Chelan, Crater, Pend Oreille and Upper Klamath) for comparison with Flathead Lake. The three first of these are deep lakes of the oligotrophic type of Thienemann (*l.c.*) while the last is a shallow lake of the eutrophic type.

The table shows a much greater number of organisms in Flathead Lake

[36] Average for all depths.
* See page 116.

than in any of the first three lakes above mentioned, while Upper Klamath is richer in some forms, (diatoms, Protozoa, Cladocera) and poorer in others (rotifers) than Flathead Lake. The lesser number of copepods in the former is probably not significant.

In western central New York are a series of lakes occupying old river valleys which, from their elongated and roughly parallel arrangement, have been called "Finger Lakes". They have been examined rather briefly by Birge and Juday (1914, 1921) and Muenscher (1928). Several of these are large deep lakes which, in their general features, resemble Flathead Lake. From them I have selected three (Canandaigua, Cayuga and Seneca) for comparison with Flathead Lake, all of which appear to conform fairly well to the oligotrophic type of Thienemann (*l.c.*). Flathead Lake shows a somewhat larger amount of plancton than either Canandaigua or Seneca, while it has more of some organisms and less of others than Cayuga.

Recently a number of studies have been made by the University of Toronto on Lake Nipigon in Ontario, about 80 km. north of Lake Superior. This is a lake approximately 4590 sq. km. in area and about 330 m. in depth. It is clearly an oligotrophic lake, although departing therefrom in certain respects; and agrees fairly well with Flathead Lake in its general features, both chemical and physical, so far as data are available for comparison. The average summer temperature of Lake Nipigon, however, is considerably lower than that of Flathead Lake, while bicarbonate alkalinity is somewhat higher. The oxygen content is high at all depths and free Co_2 varies from 0 to 1 ppm., conditions very similar to those in Flathead Lake, as is also the pH value.

I have no data on plancton abundance in the deeper parts of Lake Nipigon, but McKay (1924) has published some on the shallow bays. These data show a somewhat larger number of rotifers but fewer diatoms and Protozoa than in Flathead Lake.

Lake Erie has at various times been the subject of much limnological work. Recently an investigation, conducted jointly by several agencies, has been undertaken "to determine the cause or causes for the decline in the fisheries", a preliminary report of which was issued in 1929 (Fish et al., 1929). Judging from the available data, Lake Erie is intermediate between lakes of the oligotrophic and those of the eutrophic type, but approaches more nearly the former. It has a distinct thermocline in summer with abundant oxygen at all depths and moderate purity, judged by the analyses of carbonate and nitrogen,[37] but depth averages and light penetration are rather low.

The data for Lake Erie are in such form that I can make no comparison of the relative number of copepods and Cladocera in it and in Flathead Lake. In respect to diatoms Flathead Lake is much higher, while the numbers of Protozoa and rotifers do not differ widely.

[37] Water from the open lake is reputed to contain only about 3 ppm. of "saline" matter. If this includes all of the inorganic salts this water must be exceptionally pure.

TABLE 12. Number of organisms pr. l. for 14 lakes.[34]

	Diatoms	Protozoa	Rotifers	Copepods	Cladocera
Flathead Lake, General average of 162 samples, plancton trap colls.	3636	58	34	16	3
Canandaigua Lake, N. Y. 8/20/10, 7/27/18. Average of 16 samples from 0 to 80 m. depth, closing net colls.	14	11	1	7	1
Seneca Lake, N. Y. 8/2/10, 8/1/18. Average of 19 samples from 0 to 170 m. depth, closing net colls.	97	17	3	14	3
Green Lake, Wis., 8/20/18. Average of 8 samples from 0 to 65 m. depth, closing net colls.	1	5	6	32	1
Lake Chelan, Wash. 8/14/11, 9/11/13. Average of 25 samples from 0 to 458 m. depth, closing net colls.	3	6	0	5	0
Crater Lake, Ore. 8/1/13, 9/5/13. Average of 24 samples from 0 to 590 m. depth, closing net colls.	7	0	1	0	0
Lake Pend Oreille, Idaho. 7/17/11, 8/28/12. Average of 16 samples from 0 to 365 m. depth, closing net colls.	0	0	0	11	3
Cayuga Lake, N. Y. 8/12/10, 7/30/18. Average of 17 samples from 0 to 120 m. depth, closing net colls.	579	264	33	5	9
Upper Klamath Lake, Ore. 7/29/13. Average of 5 samples from 0 to 10 m. depth, closing net colls.	7877	1064	1	10	7
Lake Mendota, Wis. 7/20, 8/8, 10/11/06. Average of 31 samples from 0 to 12 m. depth, pump method.	....	..	233	78	..
Lake Erie, N. Y. 8/15 - 9/14/28. Average of 144 samples, net colls.	264	113	30	..	..
Devil's Lake, N. D., 1911 - 1923. Average of approximately 300 samples ([35]), Sedgewick-Rafter Method.	....	..	350	228	..
Lake Nipigon, Ont., 6/1922–9/1923. Average of 86 samples, from 0 to 22 m. depth, closing net colls.	668	27	46	15	4
Lake Neuchatel, Switzerland. 1900 - 1920. Average of 85 samples from 0 to 80 m. depth, net colls.	....	..	56	7	0

[34] In computing the averages for diatoms and Protozoa, I have omitted the filamentous diatoms and colonial Protozoa.

[35] The data on which the averages for Devils Lake were based have been lost. Furthermore, they varied somewhat for each group. Therefore the number of samples given is only approximate.

It should also be noted that, whereas the great majority of phytoplanctonts in Flathead Lake are diatoms, in both Lakes Erie and Nipigon there is a considerable proportion of other algae.

The main limnological work in North America has been done by Birge and Juday (1911, 1922) and their co-workers on the Wisconsin Lakes, most of which are relatively shallow lakes, with a depth of less than 25 m., while only one, Green Lake, has a depth of more than 60 m. I have selected two of these for comparison—Mendota and Green Lake.

The former of these approaches most nearly the eutrophic type of Thienemann with low transparency, absence or great reduction of oxygen at the bottom in late summer and early autumn, rather high plancton productivity, and presence of Corethra. But Tanytarsus, which is characteristic of the oligotrophic type, is also present in Mendota. Green Lake, on the other hand, appears to conform more nearly to the oligotrophic type, being relatively deep, with a moderate amount of plancton, and oxygen present at all depths, though much reduced at the bottom in late summer and early autumn. In comparison with Flathead Lake, Mendota shows much larger amounts of plancton and Green Lake considerably less, except in the case of the Entomostraca, which are somewhat more numerous in the latter.

We turn now to a brief consideration of a distinctly eutrophic type of lake, Devils Lake, North Dakota. This is a shallow lake whose level fluctuates considerably from year to year, but which, in 1920, had a maximum depth of approximately 6 m., while at the place where the work was done the depth was between 4 and 5 m. It is a highly alkaline lake with a total solid content in 1923 of 15,210 ppm. The bottom is covered with a layer of decaying ooze. The water is kept in more or less constant circulation by the wind, but in winter, when the lake is ice-bound, and after a few still, hot days in summer the oxygen in the bottom water is greatly reduced or entirely absent. There is an abundant growth of Ruppia and Cladophora in much of the lake. The great number of rotifers and Crustacea is clearly shown in Table 12.

I have been able to find very few data for foreign lakes which are in any way comparable to our own for Flathead Lake. The most extensive which I have found are those of Robert (1919) for Lake Neuchatel, which are given in Table 12. This is one of the larger, lower alpine lakes, which conforms to the oligotrophic type of Thienemann, and which resembles Flathead Lake in its general features rather closely. Bearing in mind the fact that the collections of Fuhrmann and Robert, upon which the latter's figures are based, were made with nets, while mine were made with the trap, which gives considerably larger amounts than the net, the results of the former collections and my own are not greatly different. Some collections from Neuchatel give larger amounts than those at similar seasons from Flathead Lake and vice versa, but in no case do the former approach in amount the collections from the latter made from April to June in 1929.

On the other hand, some of the figures given by Thienemann (1925, p. 186) for the Baltic lakes surpass any of those for Flathead Lake. Thus on March 21, 1924, there were 200,000 Stephanodiscus pr. cc. in the Eutin Lake, and on July 27, 1924 in the Pinn Lake Dictyosphaerium reached the enormous number of 700,000 cells pr. cc. But, as Thienemann says, these cases are exceptional. According to this author, in the Eifel region of Germany the deep lakes of the sub-Alpine type never show a higher plancton concentration than 1000 "individuen" pr. 1., while those of the shallow (Baltic type) may reach a concentration, even beneath the ice, of more than 100,000 pr. 1.

In the Swiss Lake of Brienz, which Flück (1927, p. 50) considers "der am dünnsten bevolkerte aller Alpenrandseen", he never found over 1800 "individuen" pr. 1. According to this author, "Bachmann gibt für den Vierwaldstattersee einen Wert von ca. 8000 Individuen pro liter." This was in November, which is not the period of maximum production in the latter lake.

Flück's figures are for the nannoplancton, obtained by centrifuging. Compared with these latter figures, those which I have given above for Flathead Lake are very high, with a maximum of over 400,000 cells (66,800 colonies) of Asterionella pr. 1. at Station 8 on July 2, 1929, and 395,000 cells (49,600 colonies) at Station 1 on April 16, 1929, and a maximum of 312,500 cells pr. 1. for Fragilaria at Station 1 on November 28, 1929.

This summary brings out clearly the relation between plancton abundance and the physico-chemical character of different lakes, and supports the contention of Thienemann (*l.c.*), Klugh (1926) and others, that the shallow type of lake with abundant vegetation is also the type with abundant plancton.

How do these lakes compare with each other in respect to the amount of their bottom fauna? Thienemann gives no adequate comparison between the bottom faunas of oligotrophic and eutrophic lakes due to lack of data for the former. Kemmerer et al. (*l.c.*) give no data for the northwestern lakes investigated by them, while the data for the Finger Lakes studied by Birge and Juday (*l.c.*, 1914) are admittedly inadequate. Muttkowski (*l.c.*) gives a table showing the distribution of 97 species[38] in Lake Mendota from the shore to a depth of 7 m., based on collections from 50 stations at each of the following depths: 0-1 m., 1-2 m., 2-3 m., 3-5 m., and 5-7 m., and Juday (1922) has given further data on the bottom fauna of this lake; while Birge and Juday (1921) have given a few data on that of Green Lake, Wisconsin, and Canandaigua, Cayuga and Seneca Lakes in New York.

Adamstone (1924) has made an extensive study of the bottom fauna of Lake Nipigon covering the years 1921-23, but during a few weeks in summer only. He also, in the same paper, gives a brief account of one series of dredgings in Lake Ontario.

[38] And 5 families of Hydracarina and an indeterminate number of leeches.

The bottom faunas of Lake Simcoe, Ontario, and Shakespeare Island Lake, situated in an island in Lake Nipigon, have been studied by Rawson (1928) and Cronk (*l.c.*) respectively. The latter is a shallow lake (12 m.) while the former is similar to Nipigon in its general features. The number of bottom animals in the latter (1568 pr. m.) is about double that in the former, while Nipigon is intermediate between them in this respect.

Eggleton (1931) has made a very thorough study of the bottom fauna of a small lake (Third Sister Lake) near Ann Arbor, Michigan, and a partial study of Douglas Lake in northern Michigan, together with some observations on Kirkville Green Lake near Syracuse, New York. The first of these is clearly of the eutrophic type with an abundant bottom fauna, while the last is a very peculiar lake, which, according to the author, is related on the one hand to the oligotrophic and on the other to the dystrophic lakes. It apparently belongs in none of the three types, but perhaps approaches the last most nearly.

Another recent investigation of interest is that of Scott *et al.* (1928) on Lake Wawasee in Northern Indiana, included in the drainage basin of Lake Michigan. It has an area of about 4,000 sq. km. and a maximum depth of 23 m. So far as I can judge from the data given, it is of the eutrophic type.

Lundbeck (1926) has given data for many north German lakes, including both eutrophic and oligotrophic types, while an extensive examination of a number of Japanese lakes, of both oligo- and eutrophic types, has recently been made by Myadi (1931, 1932) and Myadi and Hazama (1932), from which I have selected two (Motosu and Yogo) for comparison.

A comparison of the amount and general character of the bottom faunas of many of these lakes with that of Flathead Lake is given in Table 13. Because of the different dates and depths of the collections, such a comparison can be of general value only. By comparing collections of approximately similar seasons and depths for the different lakes, however, we can obtain a fair comparison of their bottom productivity.

A study of fresh water lakes shows that the underlying factor determining the abundance of life in lake as on land is food. The ultimate source of the food of aquatic and terrestrial organisms is the same—namely, the chemical elements dissolved in water; although in the case of terrestrial life, the air contributes a large part of the necessary carbon and oxygen. The chemical elements in the lake or river are in turn derived from rain water, which leaches the soil of their drainage basins. In the case of the lake, much of the food of the unicellular life—bacteria, algae and Protozoa—is derived from the larger vegetation, which flourishes best in shallow water; so that the depth of the lake, as Klugh (1926) has said, is perhaps the most important factor in determining the abundance of its life. Such a principle, of course, has its limitations. It is not to be expected that a hot spring, or a shallow pool at the base of a glacier, which is free from ice for only a few weeks

TABLE 13. Comparative abundance and depth distribution of the bottom fauna of 14 lakes in number of animals per square meter.

LAKE	Depth in Meters	Turbellaria	Nematoda [30]	Oligochaeta	Hirudinea	Crustacea	Chironomidae	Culicidae	Total Insects [40]	Hydrachnida	Sphaeridae	Gastropoda	Total Molluscs	Total Fauna
FLATHEAD	1–3	3	....	....	3	61	43	....	83	3	54	51	105	258
	6–10	4[32]	....	53+4[33]	11	119	758+2[33]	....	794	25	169	32	201	1207
	14–18	....	3	38+3[33]	9	....	423+6[33]	....	423	9	25	6	31	513
	23–36	2	25—27[32]	27+7[32-33]	....	....	171+4[32-33]	....	171	7	11	....	11	243
	49–55	8	96	....	....	....	96	....	96	....	....	....	....	200
	83–94	....	632	28	....	....	56+12[33]	....	56	....	4	....	4	720
	Average[31-39]	3	97	29	8	95	308	....	323	12	60	30	78	645
CANANDAIGUA	20	....	....	1420	....	977	....	....	800	....	....	....	....	3197
	74	....	....	890	....	844	....	....	45	....	....	....	....	1779
	Average	....	....	1155	....	910	....	....	422	....	....	....	....	2487
CAYUGA	34	....	....	....	....	178	....	....	133	....	....	....	....	311
	113	....	....	1288	....	710	....	....	3863	....	....	....	....	5861
	Average	....	....	644	....	444	....	....	1998	....	....	....	....	3086
SENECA	32	....	....	5240	....	1110	....	....	89	....	....	....	....	6439
	47	....	....	1330	....	844	....	....	577	....	....	....	....	2751
	110–172	....	....	843	....	244	....	....	244	....	....	....	....	1331
	Average[39]	....	....	2064	....	610	....	....	288	....	....	....	....	2962
GREEN	45	....	....	1480	....	6882	....	....	74	....	....	....	....	8436
	66	....	....	1643	....	459	....	....	407	....	....	....	....	2509
	Average	....	....	1561	....	3670	....	....	240	....	....	....	....	5471
ONTARIO	12	....	....	192	....	16	....	....	576	....	....	....	1856	2640
	31	....	16	2512[42]	....	32	....	....	288	....	....	....	176	3024
	54	....	32	368	....	448	....	....	16	....	....	....	192	1056
	85–93	....	104	64	....	440	....	....	8	....	....	....	128	744
	113–125	....	48	8	....	40	....	....	....	....	....	....	8	104
	Average[39-41]	....	50	459	....	208	....	....	224	....	....	....	393	1334
WAWASEE	3	14	....	10	28	1157	169	2	300	....	7	243	250	1759
	5–9	2	....	5	9	125	223	9	296	....	88	91	179	616
	11–19	....	....	32	1	....	740	185	939	....	157	8	165	1137
	21–23	....	....	....	....	....	332	258	590	....	77	....	77	667
	Average[39-41]	4	....	21	8	307	473	135	642	....	110	62	172	1154
THIRD SISTER	5–10	....	....	4323	....	....	2219	853	3072	247	....	....	....	8124
	11.5–15	....	....	7731	....	....	1007	8923	9930	49	....	....	....	17743
	16–18	....	....	577	....	....	274	25604	25878	15	....	....	....	26472
	Average[39-43]	....	....	4136	....	....	1308	10324	11632	127	....	....	....	16126
MENDOTA	0–3	....	1	367	5	114	119	....	330	75	....	....	137	1029
	3–7	....	....	1090	7	184	120	5	179	48	....	....	299	1807
	Average[39-41]	....	1	656	6	142	120	2	269	64	....	....	202	1340

TABLE 13. *Continued*

Lake	Depth in Meters	Turbellaria	Nematoda [39]	Oligochaeta	Hirudinea	Crustacea	Chironomidae	Culicidae	Total Insects [40]	Hydrachnida	Sphaeridae	Gastropoda	Total Molluscs	Total Fauna
Nipigon	0–30	....	....	86	....	118	517	....	576	....	....	....	274	1054
	30–60	....	....	36	....	224	183	....	188	....	....	....	82	530
	60–90	....	....	19	....	402	103	....	103	....	....	....	20	544
	90–150	....	....	56	....	905	59	....	60	....	....	....	2[illegible]	1047
	150–210	....	....	60	....	726	139	....	140	....	....	....	7	933
	210–390	....	....	218	....	1078	84	....	84	....	....	....	27	1407
	Average[39]	....	....	129	....	806	131	....	136	....	....	....	46	1117
Madu	Average	....	....	1665	....	....	157	....	157	....	151	....	151	1973
Greater Lake Of Plon	Average	....	....	305	....	....	171	....	171	....	68	....	68	544
Motosu	23–38	....	....	227	6	....	422	....	422	....	....	....	6	661
	40–60	10	....	104	....	....	114	....	114	....	....	....	....	228
	66–89	....	10	187	....	42	83	....	83	....	52	....	52	374
	97–119	3	....	208	....	28	184	....	184	....	15	....	15	438
	Average [39-41]	3	3	194	6	19	212	....	212	....	15	....	17	448
Yogo	0–3	....	....	23	....	....	19	....	20	....	....	....	164	207
	3–6	....	....	53	....	....	102	1	104	....	....	....	100	257
	6–10	....	....	179	....	....	174	306	485	....	....	....	18	682
	10–13.5	....	....	415	....	....	82	1638	1720	....	....	....	....	2135
	Average[39-41]	....	....	201	....	....	112	592	706	....	....	....	70	977

in summer, will furnish an abundance of life equal to that of a temperate lake. But, other things being equal, and within reasonable limits, the law holds good that the deeper the lake the less the average amount of life which it contains.

Closely allied with depth and largely dependent thereon is temperature. Within certain limits the higher the average temperature of a lake and the longer its summer season, the greater will be its productivity. As we have already seen,* however, the periods of maximum plancton abundance do not, in general, coincide with the warmest season, and especially is this true in the case of diatoms, which have their maximum development in Flathead Lake in May, when the temperature ranges from 4° to 8°. Other investigators

[39] Averages based on all collections taken separately, some of which have been combined in the tabulation, as indicated in the depth column.
[40] Includes a number of forms besides those listed in the table.
[41] Averages based on maximum depth given in table for each species.
[42] "The remainder of the material was left overnight, with the result that a great many Oligochaeta disintegrated." (Adamstone, 1924).
[43] The averages for Third Sister Lake include a number of forms listed by Eggleton as "all others", and not included in this table.
* See page 120 *et seq.*

have noted the same relation, although in general their temperatures are somewhat higher than these.[44]

Eggleton (*l.c.*) has shown also that the maximum production of benthos in Third Sister Lake, Michigan occurs in winter, and the minimum production in late summer or early autumn. There are so many factors involved in determining the amount of life in a lake that to attempt to relate it exclusively to one of these is an absurdity.

Steuer (1910, p. 606) points out that the lakes of northern Germany and, in part, of Norway have a much greater plancton productivity than do those of the Alps, of Istria or of the Balkans; apparently overlooking the fact, however, that the character of the lake itself determines its productivity and that latitude, in itself, has nothing to do with it. Furthermore, it is impossible at present to make any satisfactory comparison of the productivity of different lakes because of the different methods of investigation employed by various workers,* and because very few lakes have been studied thoroughly enough to give an adequate idea of what their productivity really is.

Not only in respect to amount of plancton and benthos, but of littoral vegetation as well, Flathead Lake belongs in the class of oligotrophic or poor-productive lakes; although it is by no means an extreme example of this class, having a much greater productivity than many mountain lakes in both Europe and America as, for example, the Lake of Brienz in Switzerland or Tahoe, Crater and Chelan in America. In point of productivity it corresponds more nearly to Lundbeck's (*l.c.*) type Al,* which is characterized by a Tanytarsus-Chironomus society and is represented by the Madü and Dratzig lakes of northern Germany and Lake Lugano in the Italian Alps.

In respect to the character of the life of any region, the determining factors are widely different in water and on land. In the first place, climatic changes on land are much greater and more sudden than in water. A priori one might expect that warm-blooded animals, like birds and mammals, would be less dependent on the temperature of their environment than cold-blooded types. And to a certain extent this is true, for reptiles are characteristically tropical, while birds and mammals range throughout all latitudes. But the factor of food, which is closely correlated with that of temperature, enters here, as does that of the rearing of young also.

Natural waters, as contrasted with air, show much smaller range of temperature. The lower limit is about 0° while the upper limit, in any lake of considerable size or depth, is seldom more than 25°, while changes take place gradually in water, so that its life is not subject to the vicissitudes of terrestrial or aerial forms.

That aquatic organisms are profoundly influenced by temperature is easily seen by comparing the life of the Labrador current with that of the

[44] Wesenberg-Lund (*l.c.*)
* See page 116.

Gulf stream, or the life of a cold mountain brook or lake, at the head waters of a river, with that of the sluggish streams and warmer lakes near its mouth. Ciscoes (*Leucichthys artedi*) are common in Green Lake, Wisconsin, but rare in Lake Mendota, while just the opposite distribution is characteristic of the yellow perch (*Perca flavescens*), a difference related by Pearse (1921) primarily to temperature. And Cahn (1927) has shown the sensitivity of the cisco to temperatures above 17° by tank experiments. In the case of fresh water life, however, so many factors enter into its environment that it is even more difficult than with land animals to determine the part played by temperature in determining its distribution.

One of the most important of these factors is the chemistry of the water. While terrestrial plants are directly affected by the chemical character of their environment (i.e. soil) the animals are, in the main, only indirectly so affected through the character of the plants upon which they feed. In water, however, both plants and animals are directly influenced by its chemical character, changes in which may produce corresponding changes in the life which it contains. Perhaps nowhere are these changes better exemplified than in Devils Lake, North Dakota, for here, in less than the span of a human life, a lake has changed so greatly in its salt content as to profoundly influence the life which it contains.

"Devils Lake is one of many lakes in the western United States, which, through lack of inlet and excess of evaporation over precipitation, is gradually drying up and steadily increasing in salt content and alkalinity. (Chemical analyses) show an increase in salt concentration, accompanying the decrease in lake level, from 8471 ppm. in 1899 to 15,210 in 1923. According to early settlers in the region, it formerly swarmed with pickerel and, until recently, the stickleback (Eucalia inconstans) was very abundant there. Lord (1884) reported a few 'shiners' and Pope (1908) stated that the minnow (Pimephales promelas) was abundant in 1907. No minnows have ever been found by me in the lake and the sticklebacks, which until 1915 were fairly common, are now much less numerous than formerly." (Young 1924, p. 28). This concentration has resulted in the exclusion of many types which are ordinarily common in fresh water—Gastropoda, Sphaeridae, Bryozoa, Macrura, Branchiura, Oligochaeta, Hirudinea, Hydrozoa and Porifera. Of these, gastropods must formerly have been numerous in the lake, as their shells have been found about the shore in recent years.

During the work of Young (*l.c.*) at the lake from 1909 to 1923, the rotifer *Triarthra longiseta* apparently disappeared, with concentration of the water above 1%, being present sparingly from 1909 to 1912 but not seen subsequently to the latter date in the lake proper; although in one of its bays, which, due to high water in 1916 was much reduced in salinity, it was reported by the late Mr. Harry K. Harring in two collections as "abundant" and "common".

In chemical character the water of Flathead Lake is in no way peculiar unless it be for its great purity, which is probably mainly responsible for the comparative paucity of its plancton and benthos. The pH values (8.21 to 8.63) show that the water is distinctly alkaline, as would be expected from the geological nature of its watershed, but I am unable to find in the character of its biota any distinct effect of this alkalinity. Mr. F. J. Myers, however, who has identified the rotifers, writes that the "collections as a whole indicate an alkaline . . . fauna . . . with the acid water species almost wanting".

In this connection the rarity of Brachionus is of interest. We have only one record, from the old outlet of the Flathead River (8/1/28). It is also of interest to note that Kemmerer *et al.* (1923), in a reconnaissance of 49 lakes in California, Oregon, Washington and Idaho, report Brachionus from one only, Medical Lake, Washington, a lake of low oxygen content and high alkalinity, and in which, according to these authors "Rotifera were especially abundant at all depths" (*l.c.*, p. 89). Furthermore, in his study of the plancton of Lake Nipigon, Bigelow (1923, p. 53) reports that "only one specimen of (Brachionus) was found during the season . . . in a small pond . . ." but not in Lake Nipigon itself. According to Harring and Myers (1928) the pH value of any water is one of the determining factors in rotifer distribution, and Haempel (1926) has emphasized the importance of this factor in determining the life of a lake. Myers (1931) lists Brachionus as a "typical alkaline-water" genus. Kemmerer et al. (*l.c.*) give no pH values for the lakes studied by them, but list several as "hard" some as "medium" and others as "soft" water lakes with respect to the amount of "fixed CO_2 content". McKay (1924) gives pH values of 7.9 to 8.4 for Lake Nipigon water, thus classifying it as a distinctly alkaline lake. Whatever may be the reason for the scarcity of Brachionus in Flathead Lake and other waters where it might be expected to occur, "there are unquestionably other factors",[45] than simply pH value involved. A similar conclusion has been reached by Behrens (1933) regarding the distribution of rotifers in the pools of East Holstein.

In Flathead Lake "The desmids, both from the standpoint of number of species and actual numbers of individuals, made up the most important part of the green algae. More species (91, representing 23 genera) and a greater number of individuals were found than all the rest of the green algae combined. They were found almost entirely in the shallow bays but occasionally a few individuals were picked up in the plancton trap. The greatest numbers of these forms were found in Hell-Roaring Bay and the mouth of the Swan River. Very few were ever found at any of the other places of collection."[29]

Wesenberg-Lund (1908) ascribes the abundance of desmids in the Irish and Scotch lakes to drainage from peat bogs or mossy mountain banks. While the number of species in these lakes is large, the number of individu-

[45] Harring and Myers (*l.c.* *p.* 675).

als is small. The Wests (1909) ascribe the abundance of desmids in the Scottish lakes to the geological formations of this region, which are older than the Carboniferous, and which fact Pearsall (1921) relates to the high ratio of sodium and potassium to calcium and magnesium in the water; while West and Fritsch (1927) ascribe their abundance to the humic acid in the water, but Murray (1905) questions this interpretation because of their abundance in the clear waters of Loch Morar and their scarcity in the brown waters of Loch Ness. It is unlikely that the age of the geological formation of any water has in itself any necessary relation to the life of that water. The chemical character of the rocks, however, undoubtedly has a very important relation thereto, through its influence on the water.

In Flathead Lake neither sodium and potassium which are much less in amount than calcium and magnesium, nor abundant rainfall, leaching humic acid out of a heavy carpet of mosses, are adequate to explain the variety of desmids there present. Here again we meet with one of those perplexing problems which are at the same time the despair and the delight of the limnologist.

A third factor which affects terrestrial and aquatic organisms differently is barriers. Excepting flying forms, such as birds and bats, and to a less extent insects, the distribution of terrestrial life is profoundly influenced by barriers. In many cases they doubtless play the major rôle in determining its distribution. With most aquatic life, however, the case is different. In whatever way these forms may be spread, whether in feathers of birds or fur of mammals, by flood or by winds, the fact remains that, excepting fish, they are much more widespread in their distribution than are most terrestrial forms, a large number of them, indeed, being cosmopolitan.

In his extensive comparison of the plancton of the lakes of the world, Wesenberg-Lund (*l.c.*) emphasizes its cosmopolitanism. He says (p. 313): "The fresh water plancton is characterized by its well-marked cosmopolitanism. Against this it can at most be said that in the high-arctic zone some types are apparently absent, that the great African lakes are characterized by their remarkable Diatom plankton and that some few genera and species (*Sida limnetica, Limnosida frontosa*) are restricted to rather limited areas; only the Diaptomidae, according to our present classification and knowledge, seem to have a distribution which is fairly sharply delimited for each species.

It must be emphasized that the fresh water plancton communities, in contrast to all other communities on land or water, everywhere contain the same types, nearly everywhere the same species. The Arctic or North European zone and the tropical zone have a very large number of species is common. This applies especially to the Diatoms, Cyanophyceae, Chlorophyceae and Flagellata; further amongst the Rotifera: *Anuraea aculeata, Polyarthra platyptera, Asplanchna Brightwelli, Triarthra longiseta,* species of the genus Brachionus, Pedalion; amongst the Cladocera: *Bosmina longirostris* and *core-*

goni, Ceriodaphnia cornuta, Daphnia hyalina, Chydorus sphaericus; amongst the Copepoda: *Cyclops serrulatus, C. Leuckarti, oithonoides,* etc. In no other community is so great a number of species common to the whole world, only very few new types are found on comparing the plancton of northern latitudes with that of southern. Considering to what a degree the different plant and animal communities, terrestrial as well as marine, change from the pole to the equator, how no end of new types appear for every degree of latitude as we proceed to the south, the cosmopolitanism of the freshwater plankton must first and chiefly be emphasized as its greatest peculiarity and one of its greatest puzzles, which we are at present unable to solve with certainty. . . .

Compared with this phenomenon the supposed maintenance of sharply delimited areas of distribution for certain fixed genera and species is of quite secondary importance. If we try by means of such areas, which appear at present apparently natural and well-defined for some species within certain groups of animals, to divide the fresh water plancton into similar well-marked zoö- and phytogeographical territories like those of other communities, we find that the attempt quite fails."

Bachmann (1924), on the contrary, stresses the individuality of lakes as follows (p. 28): "Schon Forel hat darauf hingewiesen, dass jeder See einen Organismus für sich darstelle. Und alle die Monographien der Schweizer seen, . . . stimmen darin überein, dass, wie ich schon früher bemerkt habe, nicht zwei Seen . . . mit einander in ihrem Pflanzenbilde identisch sind."

These two views are, however, by no means contradictory. True it is that the plancton, as a whole, *is* cosmopolitan. But it is also true that every lake and pond has its own peculiarities in physical and chemical conditions, which in turn determine its life, so that the latter is as variable as the former; and any attempt, such as that of Dodds (1920 *et al.*) whch seeks to bring the distribution of aquatic, into line with that of terrestrial life on the basis of one factor, i.e. altitude (temperature), but fails to consider the manifold other factors in the environment, is wholly inadequate to explain such distribution.

If we compare the life of the oligotrophic lakes of North America and Europe, we find in one the diatoms predominant among the algae, in another the blue-green, and in another the green algae. In one lake desmids are common, in another rare. In one lake Diaptomus is the principal copepod, in another Cyclops, and in yet another Epischura. There is one group, however, certain members of which are practically universal in their distribution—the "cosmopolitan group of rotifers" of Wesenberg-Lund (*l.c.*). That lake is indeed exceptional in which Anuraea, Notholea, Triarthra, Polyarthra and Asplanchna are not present.

That the life of Flathead Lake is not constant, but changing is apparent from the statement of Forbes (1893, p. 237) that "four-fifths to nine-tenths of the product of every deep-water haul with the surface net" was com-

posed of Daphnia thorata (longispina), whereas, at the present time, this form is far inferior in numbers to Cyclops and usually to Diaptomus. According to Forbes, also, Epischura was much commoner than Diaptomus, which latter "was not certainly seen at all in Flathead".[46]

A similar observation has been made by Eddy (1927) regarding the occurrence of Epischura lacustris in Lake Michigan, which, while common forty years ago, was lacking in recent collections. Eddy, however, found that in general the life of Lake Michigan today is the same as that of forty years ago. Marked changes in the plancton of the Red Lake, a small lake near Luzern, Switzerland, are also described by Bachmann (1931); and Wesenberg-Lund (*l.c.*, p. 293) says "Even in the twenty years during which I have studied the plancton in a few lakes, I believe I have seen forms die away and new arise".

Thienemann (1925, p. 179) also says "In anderen Seen stachen die Unterschiede noch greller hervor: der Schohsee erzeugte in Herbst 1921 eine Oscill, rubescens-Wasserblute; 1 Jahr später war dort kein Faden aufzufinden. Im Vierersee war das Tiefenwasser im Herbst 1921 rötlich gefärbt durch Thiorhodaceen. Im Jahre darauf konnte dort keine Zelle nachgewiesen werden; wohl aber waren Einsenbakterien an derselben Stelle vorhanden." Similar cases are cited by Minder (1926) for the Lake of Zurich and by Lundbeck (1926) for several North German lakes, and doubtless could be found in any lake which was studied for several years.

In the case of the Red Lake above cited, as in that of Devils Lake, North Dakota,* these changes are undoubtedly due to changes in the chemistry of the water, but in other cases no such explanation is available.

Regarding the origin of the life of Flathead Lake, but little can be said. Its vertebrates, apart from some introduced forms, are clearly part of the fauna of the western slope of North America, while its plants and invertebrates are, in general, species of wide distribution, indicating the effect of the Rocky Mountain barrier upon the former and the absence of such influence upon the latter.

SUMMARY

In this paper I have endeavored to set forth the composition of the life of Flathead Lake together with the factors of its physical environment, as representative of the many mountain lakes of western North America. My work indicates that the lake is of the oligotrophic type—a deep, pure, cold mountain lake with a correspondingly low productivity of plancton and benthos. Factors determining the character and distribution of the life of lakes are discussed and questions raised regarding their correlations and the origin of lake biotas in general.

LA JOLLA, Calif.

[46] In comparing our results with those of Forbes it should be noted that his collections were made in only one part of the lake, and on a single day, so that too much weight cannot be placed on the comparison.

* See page 154.

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THE BIOLOGY OF THE THATCHING ANT, *FORMICA RUFA OBSCURIPES* FOREL, IN NORTH DAKOTA

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CONTENTS

THE BIOLOGY OF THE THATCHING ANT, *FORMICA RUFA OBSCURIPES* FOREL, IN NORTH DAKOTA

I. INTRODUCTION

The thatching ant, *Formica rufa obscuripes* Forel, is widespread in North Dakota and lives in conspicuous thatched mounds. I have been able to find in the literature only one reference to it in North Dakota (McCook, 1884). Specimens of ants from nests at Jamestown were sent to Rev. McCook by R. G. DePuy, M.D. McCook called these *Formica rufa* and the description of the mounds leaves no doubt that they were *obscuripes*. DePuy's measurements show heights of mounds varying from eight inches to one and one-half feet and what was probably the brood chamber was occupied by "a ball of twigs, about eight inches in diameter." DePuy reports that there were never more than three openings, usually near the summit. He found chambers extending down as far as he dug, four and a half feet. Apparently his observations were made in the fall or early spring as the ground was already frozen.

McCook reports conversations with another resident, Mr. B. S. Russell, to the effect that numerous swarms of "flying ants" appear from late July into September and erroneously assumes that they were *obscuripes*. I have seen many swarms of winged ants which were much smaller than *obscuripes* and were of species of *Myrmica* and *Lasius*. Frequent inquiries of residents of the state have invariably brought the statement that the swarms of winged ants are the smaller ants which I have seen. A swarm of winged ants as large as the male and female *obscuripes* would be very conspicuous.

Mr. Russell also mentions the damage to the thatch mounds by prairie fires which "burn them quite up, and penetrate far enough beneath the surface to leave a hole that would contain a bushel-basket!" McCook states that the nests frequently are protected from prairie fires by "a narrow belt of smooth soil [which] generally surrounds the base of a hill, on the outer margin of which springs up a circle of tall, stiff, thick-stalked grass. . . ." "This grass remains green until late in the fall, and when the dry prairie is swept by the flames, it stands as a breastwork around about the mounds, often deflecting the fire or greatly modifying its destructive effects. In this way the formicaries are kept safe within the girdling ranks of the friendly plant." My studies do not bear out this statement. I have found several nests surrounded by dense grass which was encroaching upon the mounds. One of these nests had been burned by a prairie fire as shown by the charred twigs within the mound. It is more probable that these margins of grasses or herbs increase the danger from prairie fires.

McCook also states that the mounds are made of "an alternation of

layers of earth and vegetable substance, the latter falling into decay in due season." Such a structure is accidental and is not found in the average vigorous nest during normal years. Soil is brought up in excavating the chambers below but is carried either to the margin of the mound or dropped in such small amounts upon the nest as to be a negligible factor in nest structure. In very dry springs, however, such as that of 1934, an enormous amount of soil is transported by the frequent winds. Much of this wind-blown soil lodges in the thatch.

This brief and none too accurate account by McCook constitutes practically all which has been published on the ant fauna of the state.

The following observations were made chiefly in McHenry County which is situated in the north central part of North Dakota, about equidistant from the Montana and Minnesota state lines and twenty-five miles from the Canadian boundary. The physiographic and biological characteristics of this county are fairly representative of the state.

This paper is a condensed and revised form of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the University of North Dakota. To Professor G. C. Wheeler, under whom this study was undertaken, I wish to express my sincere appreciation of his generous assistance. I am also indebted to Dr. E. A. Baird, Professor of Botany at the University of North Dakota, for aid in the determination of plants and to Professor W. M. Wheeler of Harvard University and Dr. Esther W. Wheeler for helpful suggestions.

II. DISTRIBUTION

Formica obscuripes is an ant of western North America. Since *aggerans* is a synonym of *obscuripes* and since the status of the variety *melanotica* is doubtful, their distribution will be given together. Wheeler (1913 and 1917) records this ant from the following states and provinces:

Wisconsin	Montana	Idaho	Manitoba
Illinois	Wyoming	Utah	Alberta
North Dakota	Colorado	Arizona	British Columbia
South Dakota	New Mexico	Oregon	Washington
Nebraska	Texas	California	

Recently it has been collected in Minnesota at Delorme, Erskine and Little Falls by G. C. Wheeler and at Mallory, Walker and Bemidji by myself. I have seen specimens in the United States National Museum from Iowa and have collected *obscuripes* at Gainsborough, Saskatchewan.

F. obscuripes is found in North Dakota from the Red River "Valley", forming the eastern boundary, to the Badlands near the western boundary. It ranges in altitude from the lowest part, the Red River "Valley", at an

elevation of about 800 feet (244 m.) to the very highest point in the state, Black Butte, at an elevation of 3468 feet (1077.7 m.).

It has been collected from the following localities in North Dakota, the collectors' initials G. C. W. and N. A. W. representing G. C. Wheeler and myself:

Walhalla (G. C. W.)	Pembina County
Niagara, Larimore (C. V. Johnson), Grand Forks and Arvilla (N. A. W., G. C. W.)	Grand Forks County
Binford (M. A. Hetland)	Griggs County
McHenry (M. A. Hetland)	Foster County
Jamestown (H. C. McCook)	Stutsman County
Leeds (N. A. W.)	Benson County
Bottineau, Lake Metigoshe (N. A. W.)	Bottineau County
Balta, Barton, Rugby (N. A. W.)	Pierce County
Towner, Upham, Norwich, Granville, Denbigh, Guthrie, Bantry, Smoky Lake, Anamoose, Velva, Drake, Round Lake (N. A. W.)	McHenry County
Minot (N. A. W.)	Ward County
Sherwood (N. A. W.)	Renville County
Dunseith (N. A. W.)	Rolette County
Butte, Washburn (N. A. W.)	McLean County
Parshall, Plaza (N. A. W.)	Mountrail County
Bismark, Sterling (N. A. W.)	Burleigh County
Denhoff (N. A. W.)	Sheridan County
Hebron, Glen Ullin (Emil Krauth), Breien, Mandan (N. A. W.)	Morton County
Yucca (N. A. W.)	Oliver County
Sentinel Butte (G. C. W.), Trotters (J. E. Goldsberry)	Golden Valley County
Bicycle (G. C. W.)	McKenzie County
Medora (N. A. W., G. C. W.), Mikkelson (J. E. Goldsberry)	Billings County
Black Butte, Amidon (G. C. W.)	Slope County

Obscuripes is found throughout McHenry County, the ants avoiding only small unsuitable areas such as the damp borders of sloughs and the wooded Mouse River Valley.

III. TAXONOMY

The ant, *Formica rufa obscuripes* Forel, belongs to the family Formicidae in the order Hymenoptera.

Formica rufa was first described by Linné in the 10th edition of his *Systema Naturae*, Volume 1, p. 580, in 1758.

The subspecies *obscuripes* was first described by Forel in 1886 (Ann. Soc. Ent. Belg. 30, C. R. p. 39) from specimens collected at Green River, Wyoming. Only the workers were described and these so inadequately that Wheeler (1912, p. 90) named the same ant *Formica rufa aggerans*. Later

(1913, p. 430) he fully described the castes of *aggerans* and (pp. 433-434) redescribed *obscuripes* suggesting that further study may show them to be the same subspecies. In 1917 (1917, pp. 535-537) Dr. Wheeler definitely cleared up this question of nomenclature by synonymizing *aggerans*. Previous to this many observers had reported *obscuripes* under the name of *aggerans* from a wide area in the western part of the United States.

Forel's original description of *obscuripes* is as follows:

Ouvrière. Long., 3, 8 à 8 mill. Très semblable à la *F. rufa i. spec.* d'Europe. Mais elle est plus petite; les grandes ouvrières sont d'un rouge plus clair et presque ou entièrement sans tache sur la tête et le thorax, tandis que les pattes et l'écaille sont d'un brun noirâtre. Les petites ouvrières sont beacoup plus foncées et tachées de brun sur la tête et le thorax. L'abdomen est mat, noir, et a une pubescence grise un peu plus forte que chez la *F. rufa i. sp.*, tandis que la pilosité est plutôt un peu plus faible.—Green River, Wyoming (Scudder).

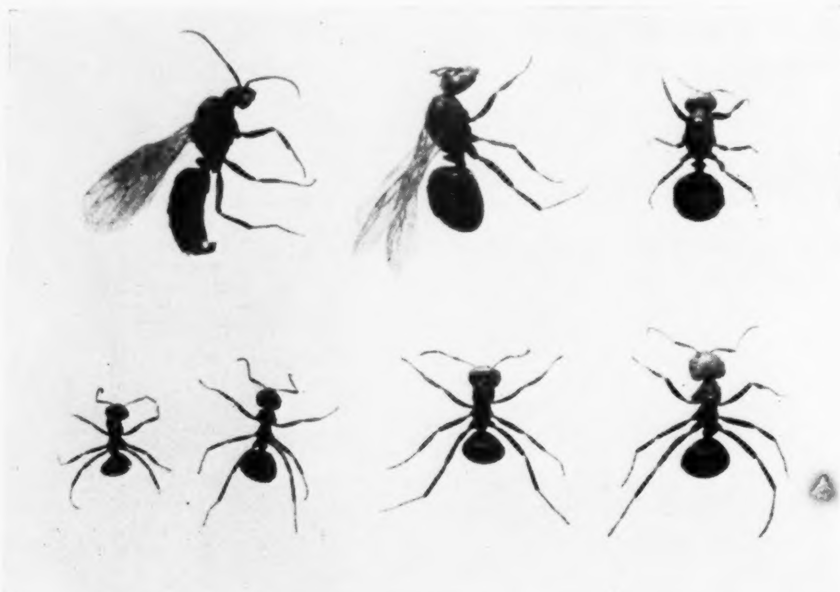

FIG. 1. *Formica rufa obscuripes* Forel. Above: winged male, winged female, queen. Below: minima, media, and maxima workers.

Emery in 1893 (Zool. Jahrb. Syst. Vol. 7, p. 650) established the variety *melanotica* as a form of *obscuriventris*:

Einige ☿ aus Wisconsin sind noch dunkler rostbraun mit mehr blutrothem Kopf.

In 1910 Wheeler (p. 570) regarded it as a variety of *obscuripes*, but in his monograph of the genus *Formica* (1913, p. 432) he transferred it to the subspecies *aggerans* and described the castes.

Representative ants from typical nests from widely separated localities in the state were sent to Dr. W. M. Wheeler in March 1932. These were all thought to be the variety *melanotica* because *obscuripes* was considered a form restricted to the Rocky Mountains and westward. Of these representative specimens Dr. Wheeler wrote, "I . . . should pronounce them all to be specimens of *Formica obscuripes* Forel. There are some color differences and perhaps the very darkest ought to be designated as Emery's variety *melanotica,* which in the large worker has the thorax black and only the head red. I am wondering, however, whether this variety has any validity, since there is such a variation in the same colony from dark minima worker up to maxima forms with rather light red head and thorax."

From my observations in North Dakota I would concur in this opinion that *melanotica* as a variety of *obscuripes* is of doubtful validity, for the following reasons:

1. Some workers from a colony may answer the description of *obscuripes* perfectly, while others of the same size from the same colony may equally well fit the description of *melanotica.*
2. Workers from one colony may answer the description of *obscuripes* while workers of the same size from a similar nest nearby may answer the description of *melanotica.*
3. All gradations of color from completely dark brown or black minima workers up to maxima workers with orange red heads and thoraces may be present in the same colony.
4. Such color differences as occur are not correlated with nest structure or habitat.

IV. ENVIRONMENT

A. Physiographic Conditions

1. North Dakota:

North Dakota includes parts of two great physiographic regions of North America, the Central Lowland and the Great Plains. The Missouri River forms the boundary between the two. For a complete account of the physiography of the state see Leonard (1919).

2. McHenry County:

McHenry County lies almost entirely in the Drift Plain of the Central Lowland, but with the Missouri Plateau crossing the southwestern corner. In general the surface of the county is gently rolling. The most striking features are the small hummocky sandhills or sand dunes which cover considerable areas, especially north, west, and south of Towner. These hills are 10 to 30 feet (3-9 m.) high and sometimes occur in irregular ranges. They are of pure sand and the tendency of the prevailing northwesterly winds is to give them a long windward slope and a sharper leeward slope.

Naturally, the binding effect of vegetation is to modify and resist the migration of these hills; but, where the cover of vegetation is scanty, the hills are true migrating sand dunes. There are a few scattered hills, as Buffalo Lodge near Granville and White Rock near Denbigh which are higher morainic hills. The rough belt of the hills of the Altamount Moraine crosses the southwestern corner.

There are no elevations in the county higher than 1800 feet (548.6 m.) above sea level, most of the county lying between 1400 and 1500 feet (426.7 m. and 457.2 m.).

The county is incompletely drained by the Mouse (or Souris) River and its tributaries, Wintering, Deep, and Little Deep "Rivers" and a number of small intermittent creeks. There are a number of small lakes, especially in the southern part, and many sloughs. Most of the lakes are "alkaline", which dry up during drouth years, leaving barren, salt incrusted, white "alkali" flats.

B. Meteorologic Condition

1. North Dakota:

North Dakota, situated as it is in the center of North America, has a truly continental climate. Temperatures in the summer of 100°F. (38°C.) to 105°F. (40.6°C.) are common and in the winter temperatures of —20°F. to —30°F. (—23°C. to —34°C.) are frequent.

The average annual rainfall for the state is slightly over 17 inches (43 cm.) and varies from 12 to 22 inches (30 cm. to 56 cm.) per year. The eastern half of the state has the highest rainfall, the Red River "Valley" being generally the wettest area. The western part of the state is the driest, averaging 10 to 15 inches (25 cm. to 38 cm.) per year. Rain falls mostly in the spring and summer months. Snowfall is light, being heaviest in the Red River "Valley" and decreasing westward. In the western part of the state the ground is frequently bare of snow in the winter for weeks at a time.

The winds are prevailingly northwestern. Winds from some direction occur most days of the year and in the spring are apt to be in the nature of violent sand or dust storms.

B. McHenry County:

McHenry County has a climate perhaps more rigorous than most counties of the state. Climatological data from the United States Weather Bureau records for Towner are typical for the county as a whole, since there are no complications due to appreciable differences in altitude, exposure, or other factors.

Maxima of 105°F. (41°C.) are not unusual and 108°F. (42.2°C.) has been recorded. Minima of —30°F. (—34°C.) in the winter are not infrequent, —49°F. (—45°C.) being the lowest recorded. Temperatures of

32°F. (0°C.) have been recorded every month of the year but infrequently in July. The ground generally freezes to a depth of 6 to 7 feet (180-215 cm.)

The average annual rainfall over a period of 30 years is 15.7 inches (40 cm.), the maximum being 28.7 inches (72.9 cm.) and the minimum 8 inches (20.3 cm.) per year. Seventy-eight per cent of the rainfall falls in the months from April to September inclusive. Snowfall is very light, the prairie generally having a very scanty covering or none at all. Snow generally forms drifts in sheltered places.

Winds are prevailing northwestern, winds from some direction occurring most days of the year.

C. Plants as a Factor of the Environment

1. North Dakota:

The vegetation of North Dakota is relatively homogeneous over the state and a clear, distinct geographical classification cannot be made. There is considerable overlapping of the different plant regions and in most places they are not sharply defined. The woodlands bordering rivers may straggle out on the prairie, particularly following up valleys. The prairie may border rivers as in the northern part of McHenry County along the Mouse River. Since altitude in itself does not exert a conspicuous effect upon the flora there are not the better defined plant zones of many regions.

For the plants of the state and their distribution reference may be made to Bergman (1912).

2. McHenry County:

The flora of McHenry County may be more readily classified since only a small area is considered. The flora may be divided into:

(1). Mouse River Valley. The valley is forested by the same deciduous trees characterizing the rest of the state, the ash (*Fraxinus pennsylvanica* Marsh.), oak (*Quercus macrocarpa* L.), box elder (*Acer negundo* L.), elm (*Ulmus americana* L.), willow (*Salix* spp.), and, in addition, dense pure stands of the quaking aspen (*Populus tremuloides* Michx.). Characteristic shrubs which I have collected are:

Betula glandulosa Michx.
Prunus americana Marsh.
Prunus virginiana (L.)
Ribes oxycanthoides L.
Amelanchier alnifolia Nutt.
Cornus stolonifera Michx.
Viburnum pubescens (Ait.)
Viburnum opulus L.
Salix discolor Muhl.
Salix longifolia Muhl?
Crataegus chrysocarpa Ashe

Herbaceous plants collected include:

Bidens cernua L.
Epilobium adenocaulum Haussk.
Helianthus maximiliani Schrad.
Helianthus autumnale L.
Helenium autumnale L.
Oxalis cymosa Small.

Mentha arvensis canadensis L.
Asclepias incarnata L.
Equisetum laevigatum R. Br.
Carex siccata Dewey?
Thalictrum occidentale A. Gray.
Vernonia fasciculata Michx.

(2). PRAIRIE. McHenry County lies in the transition between the short grass and long grass prairie and the plants would thus be somewhat representative of the state. In addition to the plants listed by Bergman for the state as a whole and characteristic of the prairie, other plants, which I have collected from the upland prairie, include:

Grasses:

Stipa comata Trin. and Rupr.
Bouteloua gracilis Lag.
Calamagrostis hyperborea Lang.
Agrostis hyemalis (Walt.) BSP.
Hordeum jubatum L.
Panicum capillare L.
Poa pratensis L.
Poa nemoralis L.
Poa compressa L.
Poa buckleyana Nash.?
Koeleria cristata (L.) Pers.
Calmovilfa longifolia (Hook) Scribn.
Andropogon furcatus Muhl.

Cacti:

Mammilaria vivipara (Nutt.) Haw.
Opuntia fragilis (Nutt.) Haw.

Herbs:

Lepachys columnaris (Sin.)
Chrysopsis villosa (Nutt.)
Solidago missouriensis Nutt.
Solidago rigida L.
Aster multiflorus Ait.
Artemesia canadensis Michx.
Artemesia caudata Michx.
Artemesia frigida Willd.
Artemesia glauca Pall.
Brauneria augustifolia (D. C.) Heller
Liatris punctata Hook.
Potentilla arguta Pursh.
Rosa pratincola L.
Anemone patens var. *Wolfgangiana* (Bess.) Koch.
Amorpha canescens Pursh.
Glycyrrhiza lepidota (Nutt.) Pursh.
Peralostemum purpureum (Vent.) Rydb.
Symphoricarpos occidentalis Hook.

The cactus, (*Mammilaria vivipara* (Nutt.) Haw.), is common over much of the dry sandy soil and prickly pear, (*Opuntia fragilis* (Nutt.) Haw.), has been found in several areas. *Bouteloua gracilis* is perhaps the most common grass and one of the more important for grazing. Wolfberry, (*Symphoricarpos occidentalis* Hook.), is a widespread shrub forming patches up to several acres in extent.

(3). ALKALI LAKES. About the "alkali" lakes and the more or less

dried flats of previous lake beds are found plants of species of the genera *Juncus, Scirpus, Carex, Chenopodium, Triglochin, Atriplex* and *Salicornia.* Away from the margins of the lakes or flats these plants intermingle with the prairie plants without forming any distinct boundaries.

(4). Sandhills. The flora of the sandhills is not strikingly different from the prairie surrounding them. The grasses and herbaceous plants are identical. The flora differs, however, in that many of the slopes of the hills, generally the north or east, are clothed with dense stands of the chokecherry, (*Prunus virginianum* L.) the wild plum (*Prunus americana* Marsh.), the Juneberry (*Amelanchier alnifolia* Nutt.), and the quaking aspen (*Populus tremuloides* Michx.). The bur oak (*Quercus macrocarpa* L.) and the box elder (*Acer negundo* L.) are commonly interspersed with other trees or shrubs. *Salix* spp. occur in clumps in the damper depressions.

V. INFLUENCE OF THE CLIMATE

A. Temperatures

Temperatures, of course, exert a conspicuous and primary influence upon the activities of these ants. Their influence may be divided into: seasonal and daily.

1. Seasonal Influence

The cold of winter necessitates hibernation and the complete cessation of all activities. Early spring is likewise too cold for activity but in normal years, early in April, the warmth of the heightening sun causes the ants to emerge. Freezing temperatures at night do no harm; the ants may be out on the nest moving sluggishly about during the day at a temperature close to freezing.

Later in the spring they are really active and commence to build up their nest and gather food industriously. Summer is the time of greatest activity, although hot weather curtails activity during the middle of the day. They maintain considerable activity in gathering food all during the fall and normally are active until well on in November. The second week in November 1931 they were slightly active during the day at temperatures from 44°F. to 57°F. (7°C. to 14°C.), though the temperatures at night ranged from 22°F. to 29°F. (—6°C. to —2°C.).

2. Daily Influence

Temperatures at night, except in the summer, are too low for activity. During the summer numbers of workers are found on the nest and even wandering about the surrounding vegetation until well into the night. The coolness of the period before dawn causes them to retire and they do not again come out until the sun's rays strike the nest.

Except during early spring and late fall the morning is the time of greatest

activity. In the early morning the ants use the sunlit nest-openings; later as the temperature rises and the sun strikes directly, they avoid the openings in the sunlight and use only those which are partially or wholly shaded by the surrounding vegetation.

In the spring and fall the middle of the day is a time of considerable activity, but during the summer little is then accomplished above the nest. When the temperature is in the eighties Fahrenheit (= around 30°C.) or higher and the sun beats directly down upon the nest without the alleviating effect of a cooling breeze there is practically no activity. A few openings of the nest may be partially shaded during these hours and only from these do ants emerge. Partly because of the desiccating effect of the sun's rays paths are constructed under and through the vegetation to the plants upon which the aphids are pastured and to hunting territory. These semi-covered runways may extend up the sides of the nest to one or two major openings. A few workers occasionally emerge to run quickly about on the mound and then go back down, as if scouting hurriedly. When a passing cloud temporarily obscures the sun, numbers of workers quickly come out and scatter about the periphery, only to return when the sun shines again. Single workers, however, have been observed on the nest even at a temperature of 103°F. (39.4°C.).

Although in the evenings during the spring and fall there is little or no activity, during the summer their evening activity is second only to that of the morning. Even after dusk they continue building and repairing the nest and foraging about for food, the temperatures remaining in the sixties or seventies Fahrenheit (15°C. to 25°C.) until several hours later.

In summary, then, the ants are most active at temperatures in the sun between 50°F. (10°C.) and 80°F. (27°C.) or in the shade between 60°F. (15°C.) and 90°F. (32°C.), provided the relative humidity is above 25%.

B. Light

In North Dakota *F. obscuripes* has a decided preference for nesting in open situations. Nests are rarely found in woods, never in dense woods, and all nests are exposed to sunlight for a large share of the time.

Full sunlight during the entire day does not curb their activities unless accompanied by high temperatures and low relative humidities. On the contrary it is conducive to their maximum activity. When the winged ants are emerging they wait for sunny periods to take flight, other meteorological conditions being favorable.

On evenings of hot days during the summer the workers are very active in food-gathering and nest-building until dusk. At these times the period from shortly before sundown to dusk is the time of activities second only to the early morning hours.

Long after dark in the summer workers are found slowly crawling about

the nest as if on patrol. Probably little is accomplished after dusk, however, as much of their prey is not moving about.

C. Winds

North Dakota lies in a region having considerable windy weather, which at times exerts an appreciable effect upon the activities of the ants.

The harmful effects of the wind are evidenced by the loosening of the thatch and even the blowing away of some of the twigs where the nest is exposed. Ants are forced to suspend their activities above ground if a strong wind, particularly when laden with dust or sand, sweeps across the nest. As noted later, winds prevent emerging of the sexual forms for the marriage flight.

D. Humidity

During the summer of 1930 I made a number of relative humidity measurements in connection with the activities of *F. obscuripes* with the following results:

The sexual forms emerged only at temperatures above ca. 60°F. (15°C.) when associated with a relative humidity above ca. 50%.

A few workers were active in shaded spots even when the relative humidity was as low as 17% at temperatures in the nineties Fahrenheit (thirties Centigrade) but were not active in the sun at relative humidities of 40% to 50% even when the temperature was 10°F. to 20°F. (5°C. to 10°C.) lower. There were no ants above the nest surface at a relative humidity of 14% when coupled with temperatures above 90°F. (32°C.).

During light rains the ants continued their activity.

In general, one might say the ants are active at relative humidities above 25% and may continue their activity at relative humidities even lower, provided they can avoid direct sunlight. The combination of the sun's rays and low humidities probably has a desiccating effect upon them.

E. Rainfall

Formica obscuripes adapts itself to considerable variations in rainfall as shown by the thriving colonies in the semi-arid western part of the state and those in the more humid Red River "Valley". That it endures the wide range in annual rainfall from 5 to 35 inches (13 to 89 cm.) shows a considerable degree of adaptability.

Drouths of a month or more during the summer do not retard activities, except when low humidity prevents the ants from being active above ground and in the sunlight during the middle of the day.

During a moderate rain the ants continue their normal activities and seem not at all hindered. Since the aphids from which they receive considerable nourishment are frequently stationed on the under surface of curled leaves, "milking" may be continued even during a rain.

F. Prairie Fires

Prairie fires are a factor of some importance in areas of the state where there is considerable grassland.

In McHenry County prairie fires are not infrequent and are detrimental in two ways: first, they set fire to the twig mound and may burn it out, resulting in a serious set-back to the colony, particularly when the brood is in that part of the nest; second, by burning the vegetation, prairie fires destroy the food of the insects forming a large part of the prey of the ants; these insects are driven out when not actually killed. The fires kill not only the vegetation upon which the aphids feed but also the aphids themselves, thus destroying the other main source of food.

VI. RELATIONS OF PLANTS AND *F. OBSCURIPES*

A. Inimical Relations

The encroachment of grasses, herbs, and shrubs constitute an ever present menace to the mound. Particularly is this true in wet seasons when vegetation is growing luxuriantly. At such times plants grow up through the nest, and the efforts of the ants are not very effective. I have seen them actually gnaw grass blades down or cut them in sections, but it is doubtful whether they could cut down large vigorous weeds, herbs, or shrubs. Later in the summer, when the nest interior is dry, the plants probably die out from lack of moisture rather than from the activities of the ants.

In the nests are sometimes found roots of shrubs which may have been killed by the ants in building up their mound. Such roots are frequently removed to form tunnels which are used by the ants to connect chambers. In one case, stout plants of the grass, *Calmovilfa longifolia* (Hook) Scribn., had kept pace with the growth of the mound for some time, as shown by their bases being from 6 to 12 inches (15-30 cm.) below the crown of the nest; while they eventually were killed off from the summit of the mound, they maintained a very heavy growth on the periphery. The overshading of plants, even when not a result of actual encroachment constitutes a second menace. Colonies are driven out of nests when such plants as wolfberry become too dense about them and shade completely.

B. Favorable Relations

Plants are of benefit to *obscuripes* colonies in three chief ways:

(1). By affording food for aphids plants are of considerable importance. The proximity of wolfberry (*Symphoricarpos occidentalis* Hook.) growths and *obscuripes* nests is not fortuitous—wolfberry is attacked by aphids which in turn afford an important source of food to the ants. Wild liquorice, *Glycyrrhiza lepidota* (Nutt.) Pursh., is similarly the host plant of the same aphid which in turn is tended by *obscuripes*. Other plants include *Populus*

tremuloides Michx., *P. deltoides* Marsh, *Salix* spp., *Artemesia cana* Pursh., *A. glauca* Pall., *A. longifolia* Nutt. and *A. tridentata* Nutt. and *Rosa pratincola* L.

(2). Plants furnish the material out of which the thatch nest is constructed. Small twigs from shrubs, grass blades, and herb stems are universally used, though in varying proportions.

(3). Plants, of course, are the ultimate source of food of *obscuripes*. The chief source of food of this ant is insects, which either feed directly (membracids, grasshoppers, and aphids) or indirectly on plants.

VII. OTHER INFLUENCES

Besides the more important influences of the climate and vegetation there are other influences at work upon the distribution or activities of *obscuripes* colonies:

(1). Physiographic Influences. As a whole, the physiography of the state is favorable to the establishment of *obscuripes* colonies. There are, however, limited areas unfavorable to them. Such areas are the steep, bare slopes of hills and buttes, chiefly in the Missouri Plateau; the damp margins of sloughs, marshes, and lakes of the rest of the state; and areas along streams subject to seasonal overflow, or at the base of buttes subject to the run-off from their bare sides.

(2). Man exercises an appreciable effect upon *obscuripes*. By cultivation of large areas of the state, he prevents the establishment of mounds in the fields and drives them to the margins. At the same time, the cultivation of crops attracts hordes of insects, particularly grasshoppers, the chief prey of the ants. The destruction of woodlands increases the nesting area, while the establishment of groves lessens the area. By bringing in herds of domestic animals he adds a new danger to the nest, i.e., trampling; but probably not of more consequence than in the days of the vast herds of bison.

(3). The influence of other animals is sometimes appreciable. The kingbird, *Tyrannus tyrannus* (L.), has frequently been observed capturing the winged *obscuripes* as they fly away from the nest. In fact one kingbird stationed itself upon a tree a short distance from an *obscuripes* nest and with great regularity captured the winged ants as they flew by, one after another. The Arkansas kingbird, *Tyrannus verticalis* Say., has also been observed near nests, feeding upon insects, presumably including the winged *obscuripes*. The flicker, *Colaptes auratus borealis* Ridgw., is a well-known ant eater. It has frequently been seen on the ground near *obscuripes* nests and is very likely responsible for holes sometimes made in the mound. Bird feces composed entirely of *obscuripes* remains were found by a nest. The common crow (*Corvus brachyrhynchos* Brehm) has been observed eating the workers.

Newly captured toads, *Bufo hemiophrys* Cope and *B. woodhousei* Girard, readily ate many workers.

Lastly, domestic animals, particularly cattle, sometimes damage mounds by tramping upon them.

VIII. THE NEST

A. Form

The form of *obscuripes* nests varies considerably from a low, almost flat, crown to a paraboloidal structure. The occasional hollowed out surface of the nest, forming a "massive rampart", described by Muckermann (1902) for *obscuripes* nests in Wisconsin has not been seen by me.

The nest is invariably a superstructure of twigs, herb stems, or grass stems constructed above the chambers in the soil. These nest materials will hereafter be referred to as thatch.

On the open sandy prairie this superstructure of thatch is frequently built upon a slight eminence of soil, which is doubtless the result of excavating the soil chambers. Among shrubs or in less sandy soil, however, the thatch superstructure rests directly on the ground.

The form of what may be termed secondary nests is similar to that of the main or primary nest except that the roots of plants furnish the nucleus about which thatch is placed and tunnels excavated. Such secondary nests are generally connected by a well-defined runway to the main nest. These roots of plants were originally preyed upon by aphids which were tended by the *obscuripes* workers. As the ants excavated the soil about the roots an arborescent chamber developed which upon the death of the plant or even while still alive, was easily made into a small secondary nest. A secondary nest may eventually develop into the chief nest of the colony.

The form of the thatched crown is always in a state of change due to the activities of the ants and to the action of the environment. The changes are brought about by:

(a). Work of the ants themselves. If there is one thing that impresses the observer of a colony it is the continuous building and repairing of the nest. Whenever any workers are above the nest surface, most of them will be engaged in altering, repairing, or adding to the thatch. They are continually changing the openings of the nest, both in number and position.

(b). Depressing action of rains and snow. The effect of rains and melting snows naturally is to level the thatch and make it more compact. While such actions are partly beneficial in that they render the nest more resistant to the elements, they are as a whole, harmful because the nest is made more susceptible to plant invasions and also is lowered with consequent shading by the surrounding plants.

(c). Destructive effect of severe winds. As mentioned before, wind-

storms are apt to loosen and even blow away portions of the thatch. Many nests, however, are protected by nearby vegetation.

(d). Destructive effects of other animals. Domestic animals, particularly cattle, sometimes trample upon the nests when grazing and damage them. Such damage, however, generally is repaired in a few days in favorable weather. Nests have frequently been observed with their openings excavated to a depth of several inches. From the circumstance that flickers (*Colaptes auratus borealis* Ridgw.) are frequently found in their vicinity and have been seen on the ground nearby and are known ant eaters it seems highly probable the openings were made by them in searching for ants.

The peculiar behavior of two pet crows indicated an unexpected factor which may, perhaps, be of some importance. These crows, entirely normal in every respect and able to fly as well as any wild ones, several times flew to the nest while I was observing the general activity. They stood upon it, fluffed out their feathers, squatted in the manner of birds taking a dust bath, and deliberately allowed the ants to crawl over them. The workers swarmed in large numbers over and through their fluffed out feathers, spraying formic acid liberally. After a few moments, when covered with ants, they hopped off the mound and shook themselves vigorously. Those ants that were still clinging to the feathers were picked off and thrown aside; none was eaten. It seemed to me the crows might have acted in this manner to disinfect themselves: the formic acid sprayed by the ants might repel the ectoparasites of the crows. The effect of this behavior to the nest was to scatter the thatch and flatten the nest appreciably.

B. SIZE

1. MOUND PROPER

The size of the mounds of *obscuripes* is highly variable. The height of the mound varies from an inch (2.5 cm.) or less in young nests to a maximum of 18 inches (45.7 cm.) in populous, flourishing colonies. The average height is about 8 inches (20 cm.) for typical nests. The diameter of the entire mound, including the soil base (when present) varies from a maximum of 11 feet 3 inches (343 cm.) to about one foot (30.5 cm.). The average typical nest is from two to three and one-half feet (60-110 cm.) in diameter. The diameter of the thatch part of the nest, alone, varies from a maximum of eleven feet (335 cm.) to a minimum of 5 inches (13 cm.), averaging about 17 inches (43 cm.). The disc area of the entire nest varies from about 98 square feet (9 sq. m.) to 0.8 square feet (0.07 sq. m.).

The thatching material extends down below the surrounding soil level to a depth of about 10 inches (25 cm.) or about 18 inches (45.7 cm.) below the top of the mound. The topmost soil chambers are made very large and close together and are filled in with thatch. The quantity of thatching material, mostly twigs, from an average nest was 0.75 bushel or 25.6 liters.

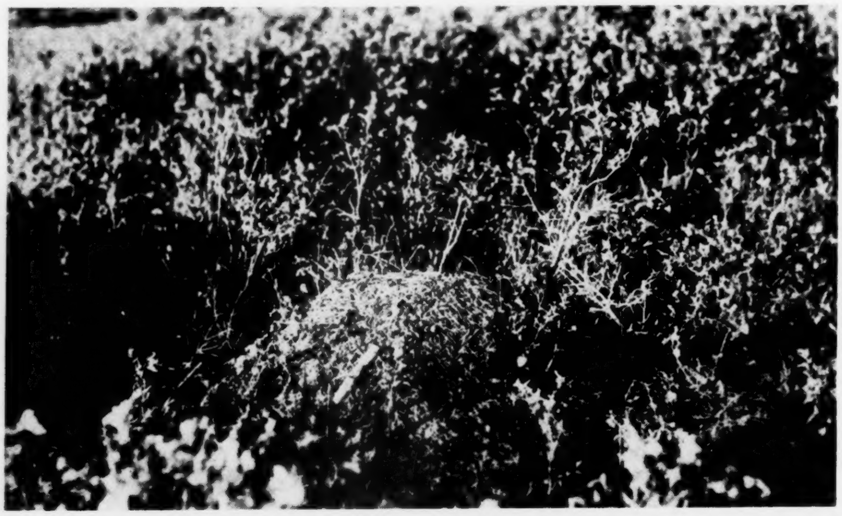

FIG. 2. Typical twig nest in *Symphoricarpos occidentalis* patch. Six inch (15 cm.) ruler at base.

FIG. 3. Nest in margin of bushes.

The thatching material has a composition varying according to the immediate plant environment. Nests in or near wolfberry (*Symphoricarpos occidentalis* Hook.) patches are of coarse wolfberry twigs mixed some finer material of grass and herb stems. Nests on the prairie at some distance from shrubs consist of somewhat finer material from grasses and herbs. Occasionally a nest is found thatched with fine grass stems which form a more compact

mound. Such nests are low and quite flat and seem to be inhabited by young colonies of small populations.

The typical *obscuripes* mounds are of coarse twigs from a fraction of an inch (1 cm.) to as much as eight inches (12 cm.) in length and usually about 1/16 inch (1-2 mm.) in diameter.

2. CHAMBERS IN SOIL

The lower part of an *obscuripes* nest, i.e., the chambers in the soil beneath the mound proper, furnishes a suitable place for the young brood and a safe place for hibernation.

FIG. 4. Young nest, showing soil periphery, at base of bushes. 6 inch (15 cm.) ruler on nest.

Chambers in the soil extend laterally less than the diameter of the entire nest but may be of greater or lesser expanse than the diameter of the thatch. Tunnels and chambers are excavated in the soil to a maximum depth of 62 inches (157.5 cm.). The minimum depth for the lowest chambers was 53 inches (135 cm.). The average depth was 57 inches (145 cm.), indicating a remarkable uniformity.

Hardness of the soil does not seem to be a serious limiting factor. In McHenry County the soil is not rocky and bed-rock is hundreds of feet below the surface. Generally the soil is sandy to a depth of several feet at least and below this it is a mixture of clay and sand. This clay-sand mixture is frequently very hard packed but penetrable by the ants.

The important limiting factor is the water table. In McHenry County it lies at a depth of 6 to 8 feet (180-245 cm.). Below about 5 feet (152 cm.), the soil is so damp that when squeezed the expressed water wets the hand.

This is apparently too wet for the ants and their chambers are never found at this depth.

C. Area Patrolled by Colony

The territory patrolled by the workers of a single colony is difficult to determine. The area can be indicated, however, by the paths which these ants make radiating out from the nest. These paths are clearly made near the nest and follow the ground closely, going beneath leaves, fallen stems, and other material so that in reality they are partially covered runways. The workers traverse these regularly in going to and from the aphids, and in bringing in prey.

On September 8, 1931, such a path was watched for two minutes from 7:36 to 7:38 A.M. at a point three to four feet (0.9-1.2 m.) from a nest. The path led to a wolfberry patch on the partially dried leaves of which still remained a few aphids. In those two minutes 11 workers passed towards the nest and 6 in the opposite direction. They were mostly minima workers and all traveled quite leisurely, keeping close to the path. A few minutes later, on the same morning, a path about 3 feet (0.9 m.) from another nest which was 90 feet (27 m.) away from the first nest was watched. In one minute 22 workers passed going towards the nest and 12 away, towards the wolfberry patch.

The maximum length to which an ant path was traced was 70 feet (21.5 m.). I have, however, found a worker 156 feet (47.6 m.) from the nearest nest. A worker was once noticed dragging a noctuid larva towards its nest, 13 feet (4 m.) away over a path which extended farther into the wolfberry patch. Paths were frequently traced three to ten feet (0.9-3 m.) from nests before being lost.

Ant paths generally lead toward areas where there is an abundance of plants upon which aphids are pastured. These paths are best developed toward wolfberry and *Artemesia glauca* patches or to the bases of *Rosa pratincola* bushes.

The extent of territory of a colony can only be very roughly estimated from such data, but it seems probable that the workers from an average colony have a territory at least of 1,000 square feet (35 sq. m.) and probably much more.

D. The Brood Chamber

In April the first brood consisting of eggs is found in soil chambers at a depth of one to two feet (30-60 cm.). Later in the spring, eggs, larvae, and pupae are found at about the same depth. It is only during the summer that the large conspicuous brood chamber is developed. This chamber, which is very incompletely divided by twigs running through it at all angles, is

generally at the base of the thatch part, resting upon the highest soil chambers. It is about 6 inches (15 cm.) high and is enclosed by thatch from 3 to 10 inches (7.6-25.4 cm.) thick. In some cases the floor is also of thatch but in others of soil. The chamber is roughly ellipsoidal in shape; one chamber measured 4 x 3 x 3 inches (10 x 7.6 x 7.6 cm.) and another 10 x 8 x 6 inches (25 x 20 x 15 cm.).

FIG. 5. Section of nest on the prairie showing central brood chamber (filled with thatch) and soil chambers beneath. Thatch superstructure is unusually compact and soil filled as a result of the severe duststorms of the spring of 1934.

Pupae and callows are kept in the upper part of the chamber while eggs and larvae are to be found in the basal part and in the uppermost soil chambers.

In the fall, after the brood has all emerged, the brood chamber is filled with thatch; hence no brood chamber is present from fall to spring.

FIG. 6. Section of nest on the prairie showing location of the brood chamber by the 6 inch (15 cm.) ruler. Thatch superstructure has an unusual amount of soil as a result of the severe duststorms of the spring of 1934.

No clear evidence was found showing that the presence of the workers or the brood raised the nest temperature. The brood chamber is so situated as to be effectively insulated and doubtless retains for some time heat absorbed during the day. During rainy periods the chamber is well drained and can dry out quickly. These are probably optimum conditions for rearing the brood.

E. Temperatures

Andrews (1927) found in the case of *Formica exsectoides* F. that inside temperatures of the nest were higher than the surrounding earth and were due to heat received from the sun.

In the case of *F. obscuripes* inside temperatures of the thatch were also found to be higher than the surrounding earth and were likely due to the heat-absorbing and heat-retaining qualities of the thatch. The presence of the brood or workers probaby had no effect upon the temperatures.

Below the thatch part there is a regular drop in temperature from the highest to the deepest chambers. The temperatures of the lower soil chambers are nearly constant all summer but show a gradual increase as the summer progresses.

F. Numbers of Nests

Formica obscuripes colonies may be absent over large areas of the state which are seemingly well suited to them and abundant in other limited areas. They do not, however, appear to be associated in such large numbers as are those of *Formica exsectoides.* It is not uncommon to find several nests a few rods (10-20 m.) apart, but additional nests are likely to be much farther away. The greatest numbers of *obscuripes* colonies found were in the sandy park-like country containing numerous, more or less continuous *Populus tremuloides* groves north of Towner. In a distance of 150 feet (45.8 m.) along the west side of such a grove were found twelve small nests. Numerous *Formica fusca* colonies were significantly present. An abundant source of food was the secretions of aphids found in great numbers on the *Populus* trees.

IX. NESTING SITES

Formica obscuripes in North Dakota is conspicuously an ant of the open and not of woodlands. The nests have always a long exposure to sunlight, many being exposed to the very maximum amount of light possible. The nesting sites chosen by *obscuripes* may be classified on the basis of the exposure, viz., those having full exposure and those having partial exposure.

A. Full Exposure

Nests having full exposure, *i.e.,* those not shaded to any appreciable extent during the entire day, are common throughout the state. Such nests are built among grasses and herbs at some distance from trees. They may be located in a great variety of places—on level or rolling prairie, in valleys, on sides and crests of hills, along roadsides, and in pastures. Dr. G. C. Wheeler has found nests upon the summits of Sentinel Butte and Black Butte (the two highest points in the state) and only a few feet from the precipitous sides.

B. Partial Exposure

While most *obscuripes* nests are built in places affording a full exposure, there are limited areas throughout the state where mounds are established in places shaded to a greater or less degree.

As mentioned before, the wolfberry, *Symphoricarpos occidentalis*, is a widespread shrub of the state, occurring in patches up to several acres in area. It is attacked by the aphid, *Aphis symphoricarpi*, and perhaps others. This aphid is frequently found tended by *Formica obscuripes* and this association of wolfberry, aphids, and *obscuripes* nests is common. Such nests are usually built in the margins of the patch and may be somewhat shaded by the shrub on one or more sides but never completely shaded.

Dense growths of grasses about the nest sometimes results in partial shading, usually of only one side. However, several nests of *obscuripes* were found completely hidden by the grass, *Calamovilfa longifolia*. The grass grew to a height of four feet (122 cm.) and completely hid the nest. In these cases the grass was probably choking out the colony.

A third condition of partial exposure is afforded by those mounds in grassy glades in groves of the quaking aspen, *Populus tremuloides*, near Towner. This association approaches the association of *Formica rufa* in the forests of Europe. Occasionally nests are shaded to some extent for a large part of the day. They are not built in locations too shady to permit a growth of grasses.

A case of partial exposure, hardly typical, was a mound found by Dr. G. C. Wheeler on the summit of Black Butte partly overgrown with the creeping juniper, *Juniperus horizontalis* Moench. Only a few ants were found in the mound and the colony was probably being crowded out by the juniper.

The sagebrush flats of the Little Missouri River and its tributaries afford a condition of partial exposure similar to that of the wolfberry. Nests are sometimes established close to the sagebrush and are protected and shaded by it on one or more sides. It is unlikely that they are ever completely shaded by the shrubs.

In the Turtle River Valley are found nests in comparatively shady situations. Here on the grassy valley floor *obscuripes* nests on the very margins of open deciduous woodlands. The shading is never dense but the trees afford some shade and considerable protection. A striking exception, however, was an enormous nest found north of Arvilla which was completely surrounded by trees. The nest received very little direct sunlight. It was distinctly not typical in shape and size as well as in location.

X. LIFE HISTORY

A. COLONY FORMATION

It has not been my good fortune to actually observe the founding of a colony of *Formica obscuripes*. However, that harbinger of colony formation, the marriage flight, has been observed in two successive summers.

Mating among ants is generally accomplished on the marriage flight or swarming of the winged sexual forms. But judging from my own observations *obscuripes* seems to have no true marriage flight. The winged sexual forms merely emerge from the nest singly or a few at a time and take flight. Fertilization by this method seems very hazardous. Local popular accounts of the swarms of winged ants always refer to much smaller ants. I have never found an observer of swarming winged ants as large as *obscuripes*.

Dr. W. M. Wheeler suggests that this situation may parallel that in middle Asia described by Kuznetzov-Ugamsky (1927). The latter states that only those ants which can modify their marriage flight to meet the harsh conditions prevailing in this steppe and desert regions are able to flourish and extend their range. The genus *Cataglyphis*, for example, has a modification of the marriage flight in which the winged sexes run about the surface of the ground and take long leaps (*Sprünge*). There is no true nuptial flight.

It may be that *F. obscuripes* in North Dakota has modified the typical marriage flight, even more than the parent stock *F. rufa*, to fertilization in the nest, or, at the most, on the ground, because of the windiness of the region at this time of year. The genus *Myrmica* forms a typical marriage flight in the same region but it takes place in late August and early September. United States government weather records show that wind movement is less in September than in June and least in August of any month of the year.

The winged males and females wait for favorable weather conditions before taking flight. When the air is calm, the sky quite clear, the temperature above 60°F. (15°C.), and the humidity above 50%, the ants take flight. In so doing they climb up a grass blade or herb stem, vibrate their wings for a moment as if to try them out, then fly upwards and are generally carried by a slight breeze until out of sight, which is a matter of 40 feet (12 m.) or more. Commonly but one or a few take flight at the same time but, whether of the same or the opposite sex, they do not fly in a group. Thus there is not the least indication of a nuptial flight. As a rule but one sex is present upon the nest at any one time, though when both sexes are present there is no interest displayed between one another. Winged ants may emerge from several nests in the same vicinity at the same time but have never been seen to fly off together. They begin to emerge early in June and may leave the nest irregularly for a month. Many of these winged ants were collected with one or

more wings crumpled or even dwarfed so that they could not fly, although they attempted to take flight in the same manner as the normal winged.

In all probability *obscuripes* follows the other Formicas of the *rufa* group in founding colonies outlined by Wheeler (1933, p. 156) by "temporary, or protelian, social parasitism". By the conciliatory type of this method the "female invades nest of the host species and is adopted by the workers after acquiring the brood and nest-odor. Host queen probably killed by her own workers". The workers "rear the successive broods of the parasite. Eventually the host species dies out and a pure colony of the parasite survives."

That this is the method likely used is supported by the coincident range of the *Formica fusca* group, the host species. Furthermore, the greatest numbers of *obscuripes* nests found by me were interspersed with numerous *Formica fusca* crateriform nests.

Muckermann (1902, p. 356) states that in Wisconsin a new colony of *F. obscuripes* is formed thus: a "little squadron sallying forth to establish a new foundation no sooner discover a warm, sunny place, than they begin to dig a few holes in the soil, when there arises gradually a little hill." He does not say whether one or more queens are brought along but I assume such must be the case. I have never seen such a "little squadron" so occupied.

B. The Brood

The brood of *Formica obscuripes* in North Dakota is probably not carried over the winter but raised to maturity between spring and autumn.

The time required for development, when kept in the laboratory at room temperature of about 63°F. and 72°F. (17°C.-22°C.), varies from 61 to 122 days. These periods agree singularly well with developmental periods found by Miss Fielde for *Aphaenogaster fulva* and by Janet for *Myrmica rubra,* as reported by Wheeler (1910, p. 81), of from 54 to 141 days and 71 to 117 days respectively.

The milky white egg is ellipsoidal, with a length of about 0.60 mm. and diameter of about 0.31 mm. Eggs have been found in nests as early as April 30, and as late as August 14. Those kept in the laboratory at a room temperature from 63°F. to 72°F. (17°C.-22°C.) developed into larvae in a minimum of 23 days and a maximum of 53 days.

Youngest larvae are of about the same length as the egg and develop to a maximum size of about 6 mm. in straight-line length. Larvae have been found in nests from June 6 to August 22. Kept in the laboratory at room temperature of about 72°F. (22°C.) they developed into the pupal stage in a minimum of 7 days. At 63°F. to 68°F. (17°C.-20°C.) they pupated after 7 to 33 days.

Male and female pupae are about 9 mm. in length, while the worker pupae vary from 3.5 mm. to 7 mm. Sexual pupae have not been found in nests later than June 20, but worker pupae have been found from June 11 to

September 9. The length of the worker pupal stage when kept in the laboratory at a room temperature of from 63°F. to 68°F. (17°C.-20°C.) was from 31 to 93 days.

The callow stage lasts only one or two days. The sexual forms and some workers scarcely have a callow stage but emerge directly from the cocoons into adults and are able to move about normally in a few hours.

C. Division of Labor

Each worker caste has fairly well-defined duties among the various activities of a colony.

Most of the activities of the minima workers are concerned with foraging and the care of the brood. Both minima and media, but chiefly the minima, workers are occasionally seen bringing up a larva or pupa from a nest opening, carrying it about for a moment, and then taking it back. While this behavior is frequently exhibited after a rain, the young do not seem abnormally moist but appear normal in every respect. The minima workers also are many times observed carrying out empty cocoons from the nest to the periphery. In short, the minima workers act as the chief nursemaids.

Workers found on the ant paths are chiefly the minima and media. They are the ones observed dragging prey to the nest and tending aphids. Very rarely is a large worker observed near an aphid colony.

While all sizes of workers take part in the building and repair of the nest, the maxima are especially active. They are, moreover, the most aggrsssive and effective in the defense of the colony, although all sizes are pugnacious and rush to its defense.

XI. POPULATION

The census of a representative *obscuripes* nest was taken in late August and early September, 1931. A rather large nest was selected which was 16 inches (40.6 cm.) high and 54 inches (137 cm.) in total diameter. The nest was surrounded and completely hidden by a dense growth of the grass, *Calmovilfa longifolia* (Hook.) Scribn., but seemed flourishing. There was another *obscuripes* nest 300 feet (91.4 m.) away, but there was no evidence of any communication between the two.

The first method used was to allow the workers to crawl upon my hand placed upon the nest, and then to brush them off into a small pail with a layer of carbon bisulphide in the bottom. While with this method many were secured at the beginning of the afternoon's collecting, the numbers of those rushing out to grasp my hand soon dwindled, and another method was then used.

Handfuls of the nest were taken up and placed in the middle of a large piece of canvas. As the ants crawled to the periphery they were picked off. This was the method generally used.

A third method was to pick up the ants individually from the nest or the cavity as I dug down.

Using these tedious methods with the assistance of several helpers, in the course of eight afternoons and a total of sixteen hours of labor most of the inhabitants were collected.

The ants, all workers, were then counted individually and a total of 16,481 was thus secured. Many cocoons and callows were dug up but were not counted since the adult population was desired. These, which would probably become adult workers in a few weeks (before the onset of winter) would probably add at least two thousand to the total inhabitants. The workers which escaped the census may have numbered 500, probably not much more. The total population of this large sized nest may thus be considered to be about 19,000.

Yung (according to Wheeler, 1913) has found for the larger nests of *Formica rufa* in Europe a population of from 20,000 to 94,000. He found, furthermore, that population of the colony did not vary with the size of the nest; the largest nest counted having scarcely half the population of the next to the smallest mound.

Until further counts of *obscuripes* are taken it may be assumed that the population of the nests will not exceed 40,000. Although in the typical *rufa* there appears to be no direct correlation between the population and the size of the nest, in the case of *obscuripes* there may be a direct relationship. Small nests have been watched and the numbers of workers about the nest are considerably smaller than those of large nests. I suspect that the size of nests of *obscuripes* indicates the size of the colony, because only a populous, flourishing colony can maintain a large twig nest. Were a small colony to occupy a large nest the numbers of workers would probably be too small to maintain the mound against the depressing effect of water and the destructive effect of winds.

XII. DAILY AND SEASONAL ACTIVITY

The daily activity of the workers varies directly with the seasons.

In the winter, since they are hibernating in the earthern chambers a few feet below the surface, there is no activity. A thaw during the winter may draw the workers in the higher soil chambers up into the twig part, but colder weather forces them down again; there is nothing they could do if they did come out.

The workers emerge early in April in average years. During the warm part of the day they come forth and slowly mill about, seemingly enjoying the warmth of the sun's rays. At first, their activity is confined to repairing the damage wrought by the snows and thaws of winter. Later, when the hordes of insects emerge, they take up the serious occupation of getting food.

At the same time they repair and build up the nest. The developing brood must be cared for and, when the weather gets warm enough, carried up into the rebuilt brood chamber.

The summer, particularly the early summer, is the time of their greatest activity. The brood requires more care, the emerging workers and sexual forms needing much attention. From early in the morning until late in the evening the workers forage about for food, taking a "siesta" only during the hottest, driest part of the day. Many are occupied in attending aphids.

During the fall they are especially active in gathering food until well on in October or November, or until all their prey is gone and the weather gets too cold. Nest building and repair takes most of the time. Only pupae are left to attend to in the early fall; after they emerge there is no brood to care for. The ants go into hibernation in November after continued cold weather or the arrival of snow.

XIII. FOOD

A. Methods Used to Obtain Data

During all hours of the day three nests at Towner were observed continuously for periods of an hour or less. At such times only a portion of the nest was in full view, because vegetation hid some of the openings on the sides. Hence, not all of the food brought to the nest at the time of observation would be seen. The food observed brought to the nest likely constituted a representative amount, however.

B. Methods Used by the Ants in Obtaining Food

The food, other than aphid secretions to be considered later, was dragged by one or more workers to the nest. In the great majority of cases the prey was already dead by the time it reached the nest. In many cases parts of insects were taken; sometimes several parts of what seemed to be the same insect were dragged successively to the nest. A specimen of *Coccinella 5-notata* Kby. was collected as it was being dragged down an opening of the nest, still alive and struggling. A *Ludius elegans* (Kby.) was also collected on a nest, still alive and struggling with a number of workers.

A possible method of capturing prey is suggested by an observation made near a nest: a worker, clinging to a grass stem, seemed deliberately to fall two or three inches (5 or 7 cm.) to a moth fluttering beneath. Although it failed to capture the moth, its behavior indicated a method which may be employed.

Upon one occasion near a nest three workers were observed investigating a membracid which was appressed to the stem of an evening primrose, *Oenothera pallida* Lindl. They climbed over and around it, touching it with their antennae; but the Membracid remained motionless, and the workers

shortly went away. If it had moved they probably would have tried to capture it.

The inedible parts of the insects used as food are either brought up and taken away from the nest, or stored in chambers within the nest. In several cases grasshopper, beetle, *Myrmica*, and *obscuripes* remains have been found stored in soil chambers between one and two feet (30-60 cm.) down the nest.

C. Natural Food

The natural food of *Formica obscuripes* was found to be derived mostly from two sources: insects and aphid secretions. Most of the insects listed below were taken from the workers as they were being brought to the nest. In many cases they were dismembered to a greater or lesser extent and sometimes seemed already partially eaten. A few spiders were also collected.

Not the slightest evidence was found to suggest that this ant might use plants as food.

1. Arthropoda

The following table, listing the arthropods used as food by *obscuripes*, includes only those specimens which I have collected directly from the workers or have found dead in the chambers of the nest. With the exceptions of the ants and spiders they were all identified at the United States National Museum.

ORTHOPTERA

Acrididae

Psoloessa delicatula? Scudd. .... adults and nymphs
Psoloessa? sp. .... nymph
Melanoplus bivittatus Say .... adult
Melanoplus sp. .... 5 small nymphs
Phoetaliotes nebrascensis Thomas .... male nymph
Acridinae .... head and thorax of adult
Oedipodinae .... small nymphs
Many grasshoppers, both adults and nymphs, which, because of their fragmentary conditions, could not be further determined.

Tettigoniidae

Orchelimum? sp. .... very small nymph

COLEOPTERA

Scarabaeidae

Dichelonyx elongata Fabr. .... 3 adults
Serica curvata Lec. .... 5 adults

Coccinellidae

Coccinella 5-notata Kby. .... adults, including a live specimen
Hippodamia parenthesis Csy. .... adult

Elateridae

Ludius elegans (Kby.) .... adults, including a live specimen

Chrysomelidae
Trirhabda sp. (*T. canadensis* Kirby?) .... adult

Carabidae
Harpalus sp. .... adult

Curculionidae
Anametis granulata Say .... adult
?Hypera .... headless pupa

Harpalidae
Harpalus herbivagus Say .... adult

Cantharidae
Podabrus? sp. .... adult

HEMIPTERA

Pentatomidae
Coenus delius **Say** .... adults
Peribalus abbreviatus Uhler .... adult
Neottiglossa undata Say .... adult

Coreidae
Alydus conspersus Montandon .... adult

Lygaeidae
Emblethis vicarius Horvath .... adult

Nabidae
Nabis subcoleoptratus Kirby .... 2 adults

Corixidae
Sp. of Corixidae .... 2 adults

HOMOPTERA

Membracidae
Ceresa bubalus (Fabr.) .... 4 adults, 3 nymphs
Ceresa sp. .... adult
Membracid .... adult

LEPIDOPTERA

Gelechiidae
Gelechia sp. .... larva

Olethreutidae
undet. larva ....

Noctuidae
Euxoa minis Grt. .... adult
Seven and possibly eight undeterminable species .... 10 larvae
Epizeuxis sp? .... larva
Feltia sp. .... adult

Tortricidae
Eucosma sp.? .... adult

Pyralidae
Pyraustinae .... larva
Crambus sp. .... adult
Thorax of moth ....

HYMENOPTERA

Braconidae

Bracon vulgaris (Cress.) .... adult

Hylaeidae

Colletes kincaidii Ckll.? .... adult

Andrenidae

Agapostemon angelicus Ckll. .... adult

Halictus (Chloralictus) pruinosiformis Crofd. .... adult

Sphecidae

Tachysphex tenuipunctus Fox .... adult

Formicidae

Myrmica scabrinodis sabuleti var. *americana* Weber (MS) .... workers and male

Lasius niger var. *neoniger* Emery .... females and worker

Lasius umbratus mixtus var. *aphidicola* Walsh .... workers

DIPTERA

Syrphidae

Sphaerophoria sp. .... adult

Asilidae

Asilus notatus Wied. .... adult

Chironomidae

Chironomus sp. .... adult

Limoniidae

Helobia hybrida Meigen .... adult

Bombyliidae

Anthrax moris L. .... adult

Sarcophagidae

Sarcophaga bullata Parker .... adult

Sarcophaga sp. .... adult

Wohlfahrtia meigenii Schiner .... adult

ARACHNIDA

Several spiders of the genera *Pellenes* and *Lycosa*.

It will be seen from the foregoing list that representatives of seven orders: Orthoptera, Homoptera, Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera include all the insect food collected.

In numbers of individuals, the Orthoptera formed the largest group, comprising about 26% of all insects taken. Most of the grasshoppers were brought to the nest in such a fragmentary condition that identification was difficult or impossible. One specimen was a tettigonid, all the rest were Acrididae. Of the latter, three genera, *Psoloessa, Phoetaliotes,* and *Melanoplus* were represented, each with at least one species. Specimens of *Melanoplus* were most numerous and include the species, *bivittatus* Say, one of the two most injurious grasshoppers of the state.

Lepidoptera formed the second largest group, comprising about 22% of all specimens. Of the five families represented, Noctuidae led with two-

thirds of all individuals. Most of the Lepidoptera were larval stages; they probably were the easiest prey of the ants.

Coleoptera constituted about 17% of all insects taken. Eight families and nine genera were represented, the genus *Serica* being the most numerous. Except for one pupa, all of the specimens were adults. Many larvae and pupae were found inhabiting the soil beneath the nest, and it is possible they are eaten if found.

About 12% of the insects were Hemiptera. Five families were represented, Pentatomidae predominating. All were adults.

Homopera also formed about 12% of the insect food. All of these were members of the family Membracidae. The destructive leaf hopper, *Ceresa bubalus*, in its nymph or adult stages constituted about three-fourths of all the specimens. No aphids were taken to the nest, either dead or alive.

Diptera constituted about 9% of the insect food. Six families were represented and all specimens were adult.

Hymenoptera formed the smallest portion, about 7%, of the insect food. Representatives of five families were present. All the specimens were adult. Only five cases of ants used as food were observed. A number of females of *Lasius niger* var. *neoniger* Emery were found in an *obscuripes* nest which had a colony of this species nesting in the margin. The position, apparently safe enough for the workers, was evidently dangerous to the sexual forms. Upon another occasion a dead worker *neoniger* was taken from *obscuripes* workers on their nest. The third case was the finding of two partially eaten workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh in soil chambers of an *obscuripes* nest. Parts of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS) workers were found in refuse chambers. The ants were probably captured as they wandered near the *obscuripes* nest. The fifth record is of a dead male *americana* taken from *obscuripes* workers on their nest.

Several medium sized spiders formed the remainder of the natural food. Small spiders are frequent inhabitants of the nest and may be eaten when found.

2. CARRION

Carrion is sometimes eaten by these ants. Richardson ground squirrels, *Citellus richardsonii* (Sabine), have several times been shot and placed upon the nest. The ants would partially eat the carcass and then bury it within the nest, as they do any object too large or heavy to move away.

3. SECRETIONS OF APHIDS

The secretions of aphids constitute an important source of food and very likely are second in importance only to the bodies of insects. It is even probable that in some cases these secretions are the primary source of food.

Jones (1929, pp. 48-50) has listed nine genera with thirty-one species of aphids tended by *Formica rufa* var. *aggerans* Wheeler, *Formica rufa*

obscuripes Forel, and *Formica rufa obscuripes* var. *melanotica* Emery in Colorado. These three forms of *rufa* are here considered to be the same subspecies, *obscuripes*. The aphids were found upon twenty-one genera of plants. Two of these genera, *Populus* and *Artemesia*, include species which are similarly associated with *obscuripes* and aphids in North Dakota.

In McHenry County, where the habits of *obscuripes* were most studied, the identified aphids found tended by them were *Aphis symphoricarpi* Thos. and *Neothasmis populicola* (Thos.). One colony of *symphoricarpi*, however, had, according to P. W. Mason, "one specimen which seems to be *Aphis medicaginis* Koch". *Aphis symphoricarpi* was frequently found on *Symphoricarpos occidentalis* Hook and on *Glycyrrhiza lepidota* (Nutt.) Pursh. in the vicinity of *obscuripes* nests. *Neothasmia populicola* (Thos.) was found in large numbers with many males present in early June, 1932 on *Populus tremuloides*.

Mr. J. E. Goldsberry found *obscuripes* workers tending aphids on sagebrush (*Artemesia* sp.) in the southwestern part of the state, which were determined by the United States National Museum as apparently an undescribed species of *Bipersona*. Unidentified aphids, tended by *obscuripes* workers, were found in considerable numbers on the leaves of many plants of *Artemesia glauca* Pall. and, of a different species, on the petioles on young shoots of a willow tree (*Salix* sp.) in McHenry County. Unidentified aphids were also found on the roots of the widespread prairie rose, *Rosa pratincola* L. and on the young leaves and petioles of *Populus deltoides* Marsh.

The relations between the aphids and ants are apparently of mutual benefit. The ants are very pugnacious and rush to the defense of the aphids when molested. While of little avail against a large enemy they probably are valuable in driving away other insects which prey upon the aphids. Coccinellid beetles and syrphid flies, among the chief enemies of aphids (Jones, 1929, p. 10), were collected as food of the ants, which is an indirect way of protecting them.

D. Food in Captivity

Workers have been kept six months or more, queens nine and one-half months, and workers have been raised from the egg stage in observation nests. The food given them was, therefore, apparently satisfactory.

Various insects have been fed to the ants in captivity with successful results. Meal worms cut in pieces were the staple insects food. Grasshoppers, moths, house flies, June beetles, and various beetle larvae were readily eaten.

Honey and sugar were the other staple foods. Apparently the ants could live for months upon either. Other sweets, such as corn syrup, maple sugar, and sorghum, proved acceptable.

XIV. MYRMECOPHILES

The myrmecophiles which I have collected from *obscuripes* nests, identified at the United States National Museum, may be classified, following Wheeler (1910, p. 380), into:

(a). Persecuted Intruders, or Synechthrans. Under this heading probably come the scavenger staphylinid beetles:

Philonthus agilis Grav.
Philonthus debilis Grav.
Philonthus theveneti Horn
Goniusa obtusa Lec.
Atheta sp.
Aderocharis corticinus Grav.
Paederinae (*Gastrolobium* or related genus)
Platymedon laticollis Csy.

(b). Indifferently Tolerated Guests, or Synoeketes. Most of the myrmecophiles which I have collected probably are of this type:

COLLEMBOLA

Unidentified small white collembolans

COLEOPTERA

Scarabaeidae	Scarabaeid pupa
Scarabaeidae	*Euphoria inda* L. in pupal cells
Scarabaeidae	*Serica intermixta* Bltch. adult
Scarabaeidae	*Phyllophaga* sp. (*P. lanceolata?*, *P. corrosa Lec.?*)
Carabidae	*Amara* sp. adult female
Elateridae	*Melanotus* sp. larvae
Chrysomelidae	*Cryptocephalus* sp. larvae
Hydrophilidae	*Berosus* sp.
Cryptophagidae	*Atomaria* sp.
Histeridae	*Hetaerius?* adult

LEPIDOPTERA

Noctuidae	*Epizeuxis* sp.? larvae

DIPTERA

Milichiidae	*Phyllomyza securicornis* Fallen larvae
Leptidae	larvae
Anthomyiidae	larvae
Therevidae	larvae

ARACHNIDA

The spiders, identified by Mr. Nathan Banks, include adults and young of both sexes of the genera *Drassus* and *Erigone*. A specimen of *Xysticus ontariensis* Emert. and a male of *Thanatus lycosoides* Emert. were taken alive in nests.

Nearly all of the above myrmecophiles were found in a single large nest.

The relations of three ants found at various times in nests of *Formica obscuripes* are not clear.

Tapinoma sessile Say workers were found in the upper 3 or 4 inches (7-10 cm.) of what seemed to be a senescent *obscuripes* nest. The interior of the nest was damp, many of the twigs were moldy and gave off a musty odor, and the whole appearance of the nest was as if abandoned. These *sessile* workers were extremely timid and avoided the light. Below this top 3 or 4 inches (7-10 cm.) of the nest a number of rather sluggish *obscuripes* workers were found. A small but flourishing nest of *obscuripes* was 600 feet (183 m.) distant.

Live workers, males and deälated alpha and beta females of *Lasius latipes* Walsh were found in digging up an *obscuripes* nest at a depth of about two feet (61 cm.). They did not seem to be captive and were possibly an independent colony.

Workers of *Leptothorax hirticornis* Emery were frequently found in *obscuripes* nests. The following excerpts from my notes upon a *hirticornis* worker, collected with *obscuripes* workers and brood and kept together in an observation nest, may suggest its relationship:

"This ant, at the approach of the large workers, flattens out as much as possible though they never seem to notice it and even walk over it." And the same morning "a worker was observed to open its mandibles threateningly at the smaller ant in its path but without further sign of hostility." Then "a worker, coming upon the smaller ant, moved nervously around, seized it violently at the same time curving its abdomen and spraying it with formic acid. The *Formica* grasped the *Leptothrax* at different places and seemed desperately trying to kill it; . . . several other workers came up and displayed hostility to the smaller ant but could not interfere because of its small size and the larger size of its attacker. Finally, the worker released it, and it crawled off, apparently none the worse although its abdomen glistened from the formic acid." The next morning this *Leptothorax hirticornis* worker was found dead. One antenna was gone, the distal part of the abdomen was cut away, and the viscera had been removed.

(c). Ectoparasites. All the ectoparasites observed were mites. These were found to be common on the sexual forms of *obscuripes* as well as on the workers. The mites, identified by the United States National Museum, include:

Parasitidae....On males, females, and workers from at least five nests.
Uropoda sp....On males, females, and workers from at least three nests.
Tyroglyphidae. Hypopi or migratory nymphs on males from at least two nests.

The mites became abundant on ants kept in the laboratory; upon a queen kept for nine months I estimated that there were over 200 unidentified mites, distributed as follows:

Posterior surface of petiole entirely covered by mites (at least 10).
About 18 on dorsal surface of abdomen.
At least 14 on each side of abdomen.
More than 50 on ventral surface of abdomen.
About 14 on dorsal surface of thorax.
At least 10 on each side of thorax.
About 5 on ventral surface of thorax.
About 10 on dorsal surface of head.
About 5 on each mandible.
Several on margin of compound eyes.
About 18 on ventral surface of head, completely lining several sutures.
At least 5 on each leg.

The only place on the queen free from mites was the antennae. The ant was rather feeble and died five days later but, whether from the mites, lack of workers to care for it, or length of time kept, I cannot say.

A common position for the mites is on the legs. On a female *obscuripes* the sole mite present was on the tibia-tarsal joint of the left metathoracic leg. Such a position is common.

XV. RELATIONS WITH OTHER ANTS

A. Relations with Ants of Other *Obscuripes* Colonies

The two *obscuripes* nests most studied were 90 feet (27 m.) apart on opposite sides of a wolfberry patch. Both had paths extending fully ten feet (3 m.) towards each other through the bushes. When workers from one colony were dropped upon the other nest they were immediately seized and attacked.

It seems probable that these are typical relations and that workers from one colony are as hostile to workers of another as if they were entirely different ants.

B. Relations with Other Ants

The relations of *obscuripes* to other ants, as far as observed, are entirely hostile.

As mentioned before, ants of two other genera, *Lasius* and *Myrmica*, were found in *obscuripes* nests in a condition indicating their use as food. Only thoraces of workers of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS) were found in refuse chambers, but a male of the same *Myrmica* variety, deälated queens and a worker of *Lasius niger* var. *neoniger* Emery and workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh were found entire or partially eaten.

XVI. COMPARATIVE ASPECTS

Our North American ant fauna is believed to have developed from forms migrating in preglacial times from Eurasia chiefly by way of Alaska (Wheeler, 1908, p. 407). Consequently we find the ant faunas of North America and Europe to be very similar. Furthermore, many of our most representative ants are merely varieties or subspecies of European species. Such an ant is *obscuripes,* a subspecies of the European *Formica rufa.*

The genus *Formica* is now found over the entire holarctic region. Its type species, *rufa,* parent stock of *obscuripes,* occurs from Siberia and the Caucasus throughout North and Middle Europe to Great Britain, south to the Pyrenees and southern Alps.

Mounds of the typical *rufa* are built of much the same materials and are of the same shape as those of our *obscuripes.* The numerous openings are similarly scattered over the whole surface of the mound. Donisthorpe (1927, p. 290) referring to *rufa* in Great Britain says: "This species nests in woods in shady places, in clearings, and on the borders of woods and forests—but also in the interior—on heaths and commons, but never far from trees, being more generally associated with fir trees, though it also occurs in oak, birch, and other woods. Forel states that in the Alps it is intimately connected with the fir trees, occurring as high as the last of these, but never higher." Nests of the subspecies *pratensis* pictured by Eidmann (1926) are in forests in rather shady situations contrasting with open exposures chosen by *obscuripes.* Indeed, the common German name of the several forms of *Formica rufa* is *die rote Waldameise,* or the red forest ant.

Yung, according to Wheeler (1910, p. 191), has found that the populations of *rufa* colonies vary from 19,933 to 93,694 individuals and that the population does not vary with the size of the mound. It seems probable, however, that in North Dakota *obscuripes* populations vary with the size of the mound, and have populations of somewhat smaller magnitudes.

The mounds of *rufa* nests are considerably larger than those of *obscuripes.* The average height, according to Donisthorpe (1927, p. 291), is about 3 feet (0.9 m.), fully twice as high as my highest *obscuripes* mound (18 inches or 46 cm.). He has recorded nests 5 feet high (1.5 m.) and a *rufa* nest pictured by Wheeler (1910) is 2.15 m. high.

The structure of the mound proper is apparently similar: "a large underground chamber, which is connected by galleries with other underground chambers and other parts of the nest" (Donisthorpe, 1927, p. 291).

The age of some of these European *rufa* mounds is known and gives an indication of the age our *obscuripes* nests may reach. Donisthorpe records a nest known to an observer for ten years, one known to himself for over twenty years, and one kept under observation by Forel for over forty years.

A comparison of the food of *obscuripes* and *rufa* is especially interesting.

Eidmann (1926) in studying the relations of *F. rufa pratensis* to the forests of Germany made many collections of the prey dragged to their mounds. His findings are similar to mine for *obscuripes*. Insects constituted the great bulk of their prey and belonged mostly to the same orders and families. These, represented in both of our collections, are: Hemiptera (Pentatomidae), Lepidoptera (Noctuidae), Coleoptera (Elateridae, Carabidae, Scarabaeidae, Coccinellidae, and Chrysomelidae), Hymenoptera (Formicidae), and Diptera (Asilidae and Syrphidae). A large proportion of the prey was coleopterous. On one occasion he collected a captured female *Lasius niger brunneus* Latr.: I found females and a worker of the North American representative, *Lasius niger* var. *neoniger* Emery, similarly used as food by *obscuripes*. He collected a very few Diplopoda and earthworms which were not found here as the prey of *obscuripes*.

Colony founding in *Formica rufa* has been observed by Donisthorpe (1927, p. 300). He saw a *rufa* female after "several fights with some of the workers" actually enter a *Formica fusca* nest. He has recorded a number of observations of his own and of others showing that the *rufa* queen may enter a *fusca* nest and be adopted by the workers. The *fusca* workers rear her brood, which eventually supplants them. In some cases the *rufa* queen decapitates the *fusca* queen. Sometimes the *rufa* queen selects a queenless *fusca* colony. Nests of *fusca* have been excavated in varying degrees of supplantation, some containing a *rufa* queen and *fusca* workers and brood, some with a *rufa* queen, *fusca* workers and both *rufa* and *fusca* brood, and others with a *rufa* queen, *fusca* workers and *rufa* brood.

Another method of colony formation is discussed by Donisthorpe (p. 292). "A certain proportion of a colony will emigrate and form a new nest with one or more queens, and a colony thus split is enabled to spread in the immediate vicinity where the conditions are favorable and the same, rather than to send off swarms to less favorable localities."

The only record of the actual mating of the sexes of which Donisthorpe was aware in 1927 was an observation made by himself in England in 1911 when he witnessed the coupling of the sexes. "A number of *rufa* males and females were seen flying about in a timber yard, running about on a large mound of sawdust in the hot mid-afternoon sunshine, flying off and settling on it, the males appearing to rise more easily than the females. Copulation took place on the mound; I never saw a single pair together in the air."

These observations on colony formation and mating of the parent stock, *rufa*, suggest strongly the methods whereby *obscuripes* colonies are founded. *Formica fusca* forms cover the range of *obscuripes* and it is very likely that *obscuripes* will be found to be a temporary parasite like its Palearctic congener.

XVII. SUMMARY

1. *Formica rufa obscuripes* Forel is a widespread ant of western North America, ranging from Illinois to the Pacific Coast states and from the western Canadian provinces to Texas. It is found throughout North Dakota from the Red River "Valley" to the Badlands.

2. The taxonomy of this ant has been confused. *Formica rufa obscuripes* Forel, *F. rufa aggerans* Wheeler, and *F. rufa obscuripes* var. *melanotica* Emery are here considered together as one form, *F. rufa obscuripes* Forel.

3. The climatic environment influences the activities of this ant in the following ways:

a. The climate of North Dakota is such that *obscuripes* is active from April to November.

b. The wide range of temperature from between —40°F. to —50°F. (—40°C. to —45°C.) to between 100°F. to 110°F. (38°C. to 43°C.) within the state is tolerated.

c. The ant thrives in regions of the state having an annual rainfall of 10 inches (25 cm.) and in regions having an annual rainfall of 30 inches (76 cm.).

d. Relative humidities below about 25% when coupled with temperatures above about 90°F. (32°C.) cause a suspension of activities. Low humidities and high temperature with direct sunshine also cause the ants to remain below the nest surface. They are somewhat active at temperatures close to freezing and at temperatures as high as 103°F. (39.4°C.), provided the humidity is moderate.

4. Plants are an important factor of the environment: as hosts of aphids tended by these ants; as the source of their nesting materials; and through phytophagous insects as the ultimate source of their food; as a menace to the nest when the vegetation is luxuriant, through encroachment.

5. *Formica obscuripes* establishes its colonies in paraboloidal thatch nests of about 8 inches (20 cm.) in height and two to four feet (60 to 120 cm.) in diameter with many underground chambers extending to a depth of nearly five feet (150 cm.). The presence of the ants and their brood has no effect upon the nest temperatures; any differences in temperature between the nest and its surroundings are due to the inherent nature of the thatch. The mounds are made of twigs, grass blades, and herb stems from the nearby plants. An important feature of the nest is a large brood chamber in the center of the thatch mound in which all the brood is kept together.

6. From a representative colony 16,481 workers were taken. An additional 500 may have escaped and the brood (cocoons and callows) probably numbered about 2,000. The population of this colony was thus about 19,000.

7. The natural food of *obscuripes* is derived mostly from two sources: insects and aphid secretions. Not the slightest evidence was found to suggest that this ant might use plants as food. Orthoptera formed about 26% of all insects taken, Lepidoptera about 22%, Coleoptera about 17%, Hemiptera and Homoptera about 12% each, Diptera about 9%, and Hymenoptera about 7%. Among the insects collected by the ants are such injurious forms as grasshoppers and leaf-hoppers. Three species of ants used as food were collected: females and a worker of *Lasius niger* var. *neoniger* Emery, workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh and a male and parts of workers of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS).

The aphid, *Aphis symphoricarpi* Thos., is tended by *obscuripes*, generally when on the wolfberry, *Symphoricarpos occidentalis* Hook. The aphid, *Neothasmia populicola* (Thos.), is tended by *obscuripes* on *Populus tremuloides* Michx.; another aphid, *Bipersona* sp., is similarly tended on sagebrush, *Artemesia* spp. The secretions of the aphids probably constitute a very important source of food. The relations between the aphids and ants are apparently of mutual benefit, the ants affording some protection in return for food.

8. Many myremecophiles live with the colony. Adults and larval Coleoptera and noctuid larvae take advantage of the favorable soil chambers for hibernation or development. Staphylinid beetles and the ant, *Leptothorax hirticornis*, may possibly prey upon the brood or isolated workers. Mites are frequently ectoparasitic upon the adults.

9. *F. obscuripes* colonies, if distinctly separated, are hostile to one another and are hostile to other ants.

10. This ant resembles its European congeners in nest structure, choice of food, and probably in life history; it differs in size of nest, population, and nesting sites.

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LAKE DEVELOPMENT AND PLANT SUCCESSION IN VILAS COUNTY, WISCONSIN*

Part I. The medium hard water lakes

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CONTENTS

INTRODUCTION

In Wisconsin, aquatic vegetation has been studied largely under the direction of the Wisconsin Geological and Natural History Survey with reference to its limnological value, and by the Wisconsin Economic Land Inventory Survey with particular reference to its economic importance to fish culture.

The first intensive ecological study made of water plants in Wisconsin was done by Denniston in 1912 (1922) on Lake Mendota. This is one of the larger lakes of the southern part of the state. It contains a variety of habitats and has very hard water. Denniston divided the lake into sections of natural units and the vegetation of each was studied and compared on a basis of specific abundance. Several years later Rickett (1922) studied Lake Mendota in detail on a quantitative basis using the same natural divisions outlined by Denniston. He attempted to determine the total amount of vegetation growing in the lake and to show its abundance on various types of soil and at various depths. He also outlines in some detail, the methods of obtaining samples, taking data, and recording results and the general methods used in the present paper were obtained there. Later Rickett (1924) investigated the aquatic vegetation of Green Lake, in Green Lake County, Wisconsin, using essentially the same methods as he had used in Lake Mendota. In this second paper he discusses more fully some of the problems of aquatic plant distribution and makes observations upon the character of the shore line. In these two hard water lakes of southern Wisconsin there are represented the general aquatic plant features of the southern part of the state.

In 1929 Fassett (1930) spent one week in northern Wisconsin in Vilas and Oneida counties making a floristic survey of nine lakes and lakelets. These range in their chemical characters from medium hard to very soft water and in their color from clear to dark. A classification of plant types roughly resembling that of Warming (1909) was suggested and the plants within nine lakes were briefly discussed.

Steenis (1931 and 1932), working under the direction of the Wisconsin Economic Land Inventory Survey, visited lakes of value to fish life in Sawyer, Douglas, and Langlade counties, collecting or recording the aquatic vegetation. In his reports he has followed the *growth form* classification of aquatic plants suggested by Fassett and has correlated his data with water chemistry. These studies have clearly brought out the fact that there are definite relationships between types of aquatic plant life and lake chemistry. They have also stressed the economic importance of the larger aquatic plants to fish.

In none of the above studies has there been any attention paid to dynamic ecology or the relationships between aquatic plant associations. This, as a subject, has not been considered intensively in the United States and very

few ecological papers are to be found that deal with specific plants in regard to the succession of aquatic vegetation. In Europe the problems of aquatic plant ecology have been more fully appreciated and valuable studies have been published (Pearsall 1918 and 1921).

During the summers of 1932, 1933, and 1934 an opportunity was presented the writer to investigate the ecology of a series of lakes in southern Vilas County, Wisconsin, under the direction of the Wisconsin Geological and Natural History Survey, with the object of determining the total plant crop in lakes ranging in development from early youth to old age. The

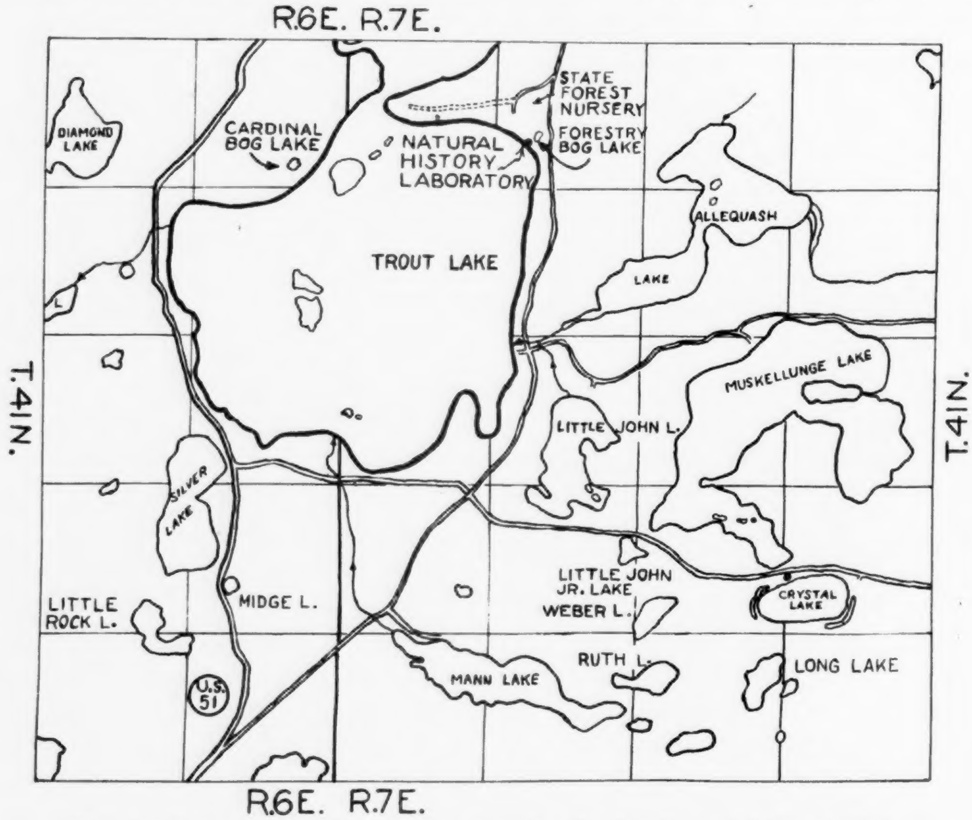

Fig. 1. General map of the region showing the location of lakes studied.

Highland Lake District of Wisconsin is particularly favorable for such ecologic studies because of the many lakes of wide range within easy access and the availability of chemical and physical data from the intensive limnological studies of Dr. E. A. Birge and Prof. C. Juday, also ample lake equipment and laboratory facilities are present (Juday and Birge 1930).

The area chosen for this study comprises about 27 square miles of Township 41 North in Ranges 6 and 7 East (Fig. 1). It contains numerous lakes of varied sizes and ecological conditions, which range from youth to old age. A series of lakes and lakelets were selected from this area that illustrate the development of a lake with its accompanied floristic history. Trout Lake

is omitted from the present paper because of its size and complexity. A detailed survey of the vegetation and shoreline has been made and the results show that though Trout Lake is the largest in the area, the problems of its ecology are like those of the others, and are probably more static due to its larger size. The series of lakes chosen are believed to be a true representation of the lake and floristic development within southern Vilas County and the adjacent regions of the same soils and glacial history.

PHYSIOGRAPHY AND SOILS

The physiography of southern Vilas County is definitely related to the Wisconsin Stage of glaciation and its topography varies with pitted and unpitted outwash plains, hills due to moraines and drumlins, and valleys, which lie between morainic features or are caused by glacial and postglacial drainage.

Beneath the glacial drift, Thwaites (1929) gives granite, gneiss and schist as the most important bed rocks and states that the relief of the bed rock surface is not very great. These rocks are essentially acid in nature and probably reflect to some degree that character in the soils of the region.

The importance of glacial activity in Vilas County is shown in the study of Thwaites, for in his discussion he makes the following statement: "The drift deposits of the area surveyed can be divided into (a) outwash, (b) terminal (recessional) moraines, (c) drumlins, (d) ground moraine, and (e) eskers. Of these, the first covers by far the largest portion of the region and the second forms the most conspicuous topographic features and the most striking country. The other features cover only an inconsequential percentage of the region."

Within the area here studied (Fig. 1) the irregular topography is due largely to the Muskellunge Moraine, ground moraine and glacial drainage, which resulted from the waters of the ice front as it rapidly melted. This moraine is very conspicuous in the southern portion of Township 41 of Range 7 and has been utilized as a location for a fire tower by the state forest service. Immediately to the north of the moraine much stagnant ice melted and formed outwash or deposited its load in the form of ground moraine, which also shows evidence of water working. The lakes were formed in depressions left by large masses of stagnant ice. The general history of the region is therefore quite simple, but the details of local conditions are often complex and are important in considering the distribution of soils. No attempt has been made to follow through the details of local glacial history of any lake except to determine the soil type and possible origin as it affects the ecological history.

The soils of the region have been studied by Whitson and Dunnewald (1915). The two most important mineral soils listed are Plainfield and Vilas in the soil series. According to Thwaites (l.c.) Plainfield soil originated from

outwash and is slightly weathered. Vilas soil is outwash with a few kames and some terminal moraine where the till is covered with a few feet of sand. It shows more alteration than the Plainfield soils.

Plainfield and Vilas soils are primarily sand and differ from one another in the quantity of gravel and sand. Each soil is divided into two or more types dependent upon texture, and the type of topography that it forms. The Plainfield soils are divided into the Sand and Fine Sand groups. Both of these are present in the area under discussion with the first as the more abundant. The Vilas soils are likewise separated into types but only the Sandy Loam phase is abundant and considered here. The two tables given below present a comparison of these two types of mineral soils. They are compiled from tables given by Whitson and Dunnewald and represent the extremes recorded by them.

Table 1. Mechanical analysis of soils in per cent

Soils	Gravel	Coarse Sand	Medium Sand	Fine Sand	Very Fine Sand	Silt	Clay
Vilas	5.75	11.74	13.84	25.64	15.25	15.08	5.75
Sandy Loam	11.73	12.59	13.91	26.54	16.04	19.30	6.60
Plainfield	2.54	14.57	21.20	27.08	4.71	4.75	3.34
Sand	9.10	22.44	30.30	37.37	9.87	9.61	9.92

Table 2. Chemical analysis of soil in per cent

Soils	Total Phosphorus	Total Potassium	Total Nitrogen
Vilas	0.041	1.20	0.030
Sandy Loam	0.064	1.57	0.103
Plainfield	0.027	0.87	0.025
Sand	0.052	1.36	0.096

The soils about and in each lake are variable and will be considered separately.

The drainage of the larger lakes of the area, as seen on the map, (Fig. 1), is into Trout Lake and thence to the Manitowish and Wisconsin rivers. If perfection of drainage be considered as an indicator of physiographic maturity, the region is in extreme youth. The processes of erosion have not perfected to any degree the drainage of Vilas County and consequently much of the former water area has developed into bog land.

THE DEVELOPMENT OF LAKES

In the subject of lake development two processes that have a profound influence on lake history and ecological conditions should be kept in mind. These are erosion and sedimentation. They are important in the development of an area to its base level, and if the climate is not too severe, the stage

to which these processes have succeeded is reflected in the vegetation of the region regardless of whether it is aquatic or terrestrial. Erosion as a process is continually at work carrying materials from higher to lower levels and cutting away the headwaters of gullies and river courses, thereby perfecting drainage. By this process materials both inorganic and organic reach their places of rest and are constantly filling up bodies of water and changing the chemical and physical characters of the lakes. In a region of physiographic youth, such as Vilas County, the drainage is very imperfect and sedimentation is the more active process. Because of the slowness of the erosional process in Vilas County, vast areas of water isolated from any drainage system will be filled with weathered peat soils by the time the region has reached maturity. Consequently erosion may be disregarded except where lakes receive a constant supply of mineral salts in the sediments which streams carry into them.

The developmental details of lakes from their origin and youth to old age and extinction is a subject that must be considered with regard to geography and geologic history of a specific region if minor generalities are to be determined. All the details of development of the lakes in Vilas County do not hold for those of southern Wisconsin or even eastern Langlade County, just 50 miles southeast, where the soils are largely derived from a limestone drift instead of sand and silt as is the condition in southern Vilas County.

A classification of Wisconsin lakes based on drainage has been in use for some years by the Wisconsin Geological and Natural History Survey. The lakes are separated into those which belong to a drainage system and those which are isolated from such a system. They are known as drainage and seepage lakes and by this simple division much can be predicted about the chemistry and physics of the water and a rough estimate of the physiographic age of a lake can be made. In a recent study (Juday and Birge, 1933) some chemical and physical characters of over five hundred Wisconsin lakes have been considered with reference to this classification. The investigation has shown that conductivity of lake waters is greater in lakes having regular drainage. The bound carbon dioxide content and hydrogen ion concentration are likewise higher in drainage lakes than in seepage lakes. These conditions seem to be retained by the constant influx of silt bearing water. From this study it is evident that the drainage lake is most likely to be the medium to hard water lake and the seepage lake the soft water lake. In using the terms hard, medium, and soft water the following scale used by the Wisconsin Geological and Natural History Survey is employed:

Soft....................	0-10 parts per million of bound carbon dioxide
Medium hard............	10-30 parts per million of bound carbon dioxide
Hard..................	over 30 parts per million of bound carbon dioxide

A deep lake in Vilas County, Wisconsin that remains part of a drainage system throughout its development, first becomes smooth in outline as the

bays fill with sediments and vegetation, and finally, swamp and bog. Further maturity is shown when sediments have filled the lake to a point where it is shallow enough for aquatic vegetation to cover nearly the entire bottom. Then a channel is developed and natural levees are formed on each side, while in back, swamp land and bog gradually form.

The stages in progressive development of a seepage lake, disregarding the specific vegetational history, is outlined in the following six steps.

(1) The lake becomes, or is originally, isolated from a drainage system.

(2) The bays are cut off from the main body of water by bars, spits, or ice pushes, forming across their mouths, and by the invasion of the land flora upon organic and inorganic sediments. The shape of the lake then becomes smooth in outline, often oval or round.

(3) Settling of the mineral salts, leaching of the mineral soils in the shallow water and around the lake, loss of electrolytes, bound carbon dioxide, and a decrease in hydrogen ion concentration.

(4) Organic sediments accumulate in sheltered places and in deeper water. There is an increase in water color.

(5) The invading land flora spreads about the perimeter of the lake developing mostly where it is sheltered from water movement, i.e., around logs, rocks, and sheltered sides of the lakes. The rapidity of further development depends upon the area, the depth, and the amount of debris blown or carried into the lake. The soils become organic.

(6) The land vegetation grows outward over the water until the area is covered by plants supported upon an organic mat. The shape of the lake again becomes irregular as it nears closure.

The Aquatic Vegetation and its Relation to Lake Types

A comparison between the terrestrial and aquatic vegetation of Vilas County shows each to have much in common with the other. The dominant vegetation of the region belongs to that of the Canadian Zone, while there are present in smaller quantities species of the Atlantic Coastal Plain flora, and terrestrial species of the western prairies.

The terrestrial flora can be divided, often very clearly, into two groups, one which grows on the rocky soils, called Vilas, and the other, on the sandy, called Plainfield soils. The climax trees found on the first are usually hard and soft maple, basswood, and white and yellow birch with the following conifers: hemlock, balsam fir, and red pine. The cut-over areas that now have a secondary growth upon them have an aspen, white birch and pin cherry cover. The climax trees of the Plainfield soils seem to have been white and red pine, but all that remains of most of these forests are large areas of stumpage. The secondary growth is dominantly aspen and white birch in the more moist places and jack pine in the dryer. The relation of soils and forest vegetation in the lake states region has been studied by Wilde (1933) and his

conclusions summarize the area of southern Vilas County very well. The Wisconsin Economic Land Inventory Survey under the direction of Bordner and Morris (1931) has mapped the cover of Vilas County and the vegetation is markedly related to the types of soil described by Whitson and Dunnwald.

The littoral flora of the region contains the usual Canadian species and also in a rather surprising abundance, species of the Atlantic Coastal Plain. Of these the more important are *Eriocaulon septangulare, Littorella americana, Juncus pelocarpus, Utricularia resupinata, U. cornuta, Rannuculus reptans, Dulichium arundinaceum,* and *Lycopodium inundatum.* The occurrence of these and others in the sand barrens of northwestern Wisconsin has been studied by McLaughlin (1932) and he concludes that their appearance in northwestern Wisconsin is associated with the Glacial Great Lakes. Just how the species found in Vilas County fit into the early history of the region is not clear. Their presence was not known when McLaughlin was working with this problem.

The aquatic vegetation likewise has its Coastal Plain element in some of the *Potamogetons,* but the stress upon aquatic vegetation in northern Wisconsin has not been so much on its history as on its *growth forms* and their distribution in the various types of lakes. The first to point out this relationship in Vilas County was Fassett (1930). He observed that a rosette type of vegetation was the dominant plant life of the soft sandy clear water lakes, and that in the more alkaline lakes the vegetation was more massive. The following *growth form* classification was constructed and in the nine lakes and lakelets in which observations were made there seemed to be some definite distribution of the four groups: (1) *Plants with long lax stems and flexuous leaves.* These species with the exception of *Utricularia* appeared to be restricted almost entirely to the more alkaline lakes of the region. (2) *Plants with stiff leaves in a close rosette or on short, rigid unbranched stems.* These species occurred more often in soft clear water lakes, but some species were also found in both bog lakes (soft water) and in the alkaline lakes. (3) *Plants with vegetative stem horizontal and the leaves mostly or entirely floating on the surface of the water.* Species of this growth form appear in all types of lakes. (4) *Plants with bases in the water and photosynthetic parts mostly or entirely emersed.* These species appeared only in lakes of medium hard water, which are the alkaline lakes of the region.

During succeeding seasons Steenis (1932, 1933) further investigated the lakes of northern Wisconsin, examining several hundred of them, and classifying the plants as was done by Fassett. He suggested a fifth class to include those species which float on the surface or sink to the bottom. These species appear to be restricted to the medium hard water lakes. The results are exceedingly interesting in the support they give to the *growth form* type of ecological classification for aquatic plants. His tables show, however, a transition of one plant form from one type of lake into another, especially if they

are examined with reference to definite species. This was not discussed by Steenis and no reference was made to dynamic conditions in lake ecology.

When the present work was begun the distinctiveness of the clear sandy outwash lakes was noted. Crystal Lake, one of those described by Fassett, belongs to this category and is one of the best examples of a lake having a rosette type of flora. Other lakes of this type were examined and additional species of plants belonging to other classes were encountered. These additional species usually occur in less abundance and in a part of the lake that is more mature than the larger portion. In further investigating the effect of lake maturity upon the vegetation it was found that certain species, such as *Sparganium angustifolium*, though often present in sandy clear water lakes was sparse until the lake or some portion of it had developed to the stage where organic sediment covered the mineral soil. When this stage had been reached, *Sparganium angustifolium* became abundant and some other species usually abundant in the clear sandy lakes were sparse or absent. Here it became clear that, though they may be classified on the basis of similarity of conditions, these lakes and their vegetation are dynamic things in which their sequence can be followed determining the ecological relationship of each species of plant to the other. The soft water lakes presented a fairly simple progressive series of stages, but when the medium hard water lakes were examined, perplexing problems were encountered. These problems when summarized centered largely about the types of sedimentation and the soils which resulted from them.

Frequently in portions of the medium hard water lakes, as in the soft water lakes, are found small areas with a distinctly different type of vegetation. Where sheltered bays exist sediments accumulate rapidly and the vegetation is often luxuriant and of the flexuous type. Where the soils are sandy and these have been leached to some extent there occur plants such as are typical of Crystal Lake. The extent to which these rosette or soft water lake species are found in a medium hard water lake appears to be the extent to which the lake, or portion of it, has become modified by the processes which produce such conditions. The question soon arose as to the source of the soft water vegetation, if it did not always exist in the lake. It is easy to account for the disappearance of a species from a lake by ecological succession but it was not clear from what source the new members were to come, if they had not previously existed there, at least in small quantities. An examination of the following important "rosette species" in the sandy clear water type of lake, suggests that *Lobelia Dortmanna, Eleocharis acicularis, Juncus pelocarpus, Gratiola aurea*, and several others, are derivatives from the beach zone. They are terrestrial plants that "go aquatic" when conditions in the lake become favorable. A detail study of this succession has been made and will be discussed at length with the soft water lakes.

METHODS

The methods used during 1932, 1933, and 1934 for the determination of plant quantities were essentially those developed by Rickett and described in his paper on Lake Mendota (1922). Several changes were made as the work progressed and a brief description of the methods are given here. In Lake Mendota and in Green Lake, Rickett collected plants from quadrates of one-half square meter by diving either with or without a hood. This was found impossible to follow in the Vilas County studies because the plants were found growing at greater depths, much beyond where a diving hood would be practical and also because the waters are too cold for extensive swimming during the entire season. Instead, a small modified Peterson dredge fitted with a heavy, calibrated, water-proofed, cotton rope was used to collect plants. This dredge is capable of denuding an area of 100 square inches or 625 square centimeters and at the same time of picking up enough soil to take specimens for laboratory examination. Another feature of this dredge is that it usually collects both roots and leafy stems making it possible to determine the entire plant crop and proportion of root and leafy stem. In the rosette type of vegetation the roots make up almost as much of the plant weight as those portions which occur above the soil.

When a lake to be studied was first visited its natural divisions were determined. Then the number of transects that were to be made through these was decided upon, though usually each division was small enough to make it unnecessary for more than one to be run. (See individual maps of the lakes studied). Where a shoreline is smooth in outline there is usually a uniform aquatic habitat to be found opposite it in the lake. Along such shorelines, especially where they cover considerable distance, transects were often made as checks upon one another.

A transect consists essentially in a profile study of the lake bottom from the shore into water beyond the outer limit of vegetation. This is made along a straight line usually through the middle of a natural ecological division in the lake. It consists of a series of quadrate collections beginning at one-fourth meter in the larger lakes and one-eighth meter in those which have vegetation in shallower water. Plants from successive quadrates were collected as the water deepened by one-fourth meter. Each collection of plants was washed free of debris in a screen especially constructed to hang over the end of the boat, and then they were packeted and labeled. Soil samples were not collected along every transect but only along those where new bottom features were encountered. The soils were carried to the laboratory in pint or gallon jars depending upon their nature, and dried by the sun in evaporating dishes.

At the laboratory the plant packets were divided into species and dried in the sun. Then each species collection was weighed and recorded.

The records consist of the air dry weights of each species from each station

and each depth at which it was collected. With this information it is possible to determine the optimum growing conditions of the various species when correlated with other studies made on the lake.

When these methods were first used in Vilas County they were tested in detail on Weber Lake (discussed in Part II). Transects were studied at intervals of about fifty meters entirely around this lake. When the results were graphed on depth and weight each species showed a remarkably smooth curve, bearing out the visual changes noticeable to anyone studying aquatic plants in this lake.

In determining the entire crop of each species in a lake the weight of all collections of that species were added together and the average weight per square meter determined. This was then multiplied by the total area colonized to determine its total crop in the lake. The area colonized by any one species was figured from the maximum depth. Such a computed area will naturally introduce some error of area, but this was corrected in part by dividing the natural divisions into two or more groups depending upon the depth of plant growth.

TABLE 3. Summary of lake characters

(From the records of the Wisc. Geol. and Nat. Hist. Surv.)

LAKE	*Total Area* (sq. kilom.)	*Max. Depth* (meters)	*Color*	*Bound* CO_2 (pts. per Mil.)	*pH*	*Conductivity*
Silver	.87	19	0	14.3	7.6	59
			8	20.0	7.8	60
Muskellunge	3.72	21	8	9.0	6.6	38
			14	10.5	8.2	53
Little John	.67	6	14	8.34	6.8	68
			22	17.20	8.4	71
Green	11.90	68	4	37.8	8.1	275
			6			
Mendota	39.40	25	14	34.2	8.7	285

SILVER LAKE

Sections 23, 24, 25, and 26; Township 41 North; Range 6 East

As is true of all other lakes observed in the region, Silver Lake has developed in a kettle hole left by the retreating Wisconsin ice front. The lake, except for a constriction near its middle, is nearly oval in outline (Fig. 2). It is about one mile long, and about one-fourth of a mile wide. The total area is 872,000 square meters and the maximum depth is 19 meters.

The topography of the surrounding upland is hilly and rugged especially on the southern and western sides. There are present at the south end of the lake several large boulders and many smaller rocks. According to Thwaites (l. c. Fig. 1), Silver Lake is in an area of outwash. If this is true, the rugged topography and the abundance of boulders indicate this to be a very thin mantle over the ground moraine.

The original shape of the lake has been altered very little, and there is a high, smooth shoreline almost entirely around the lake. Several low places and irregularities were present when the lake was first formed and at these the following changes have taken place.

At the southeast corner of the lake the water originally extended into a small bay. Sediments carried by various agencies, especially longshore currents, have filled the mouth of this bay with sand. Ice action has caused

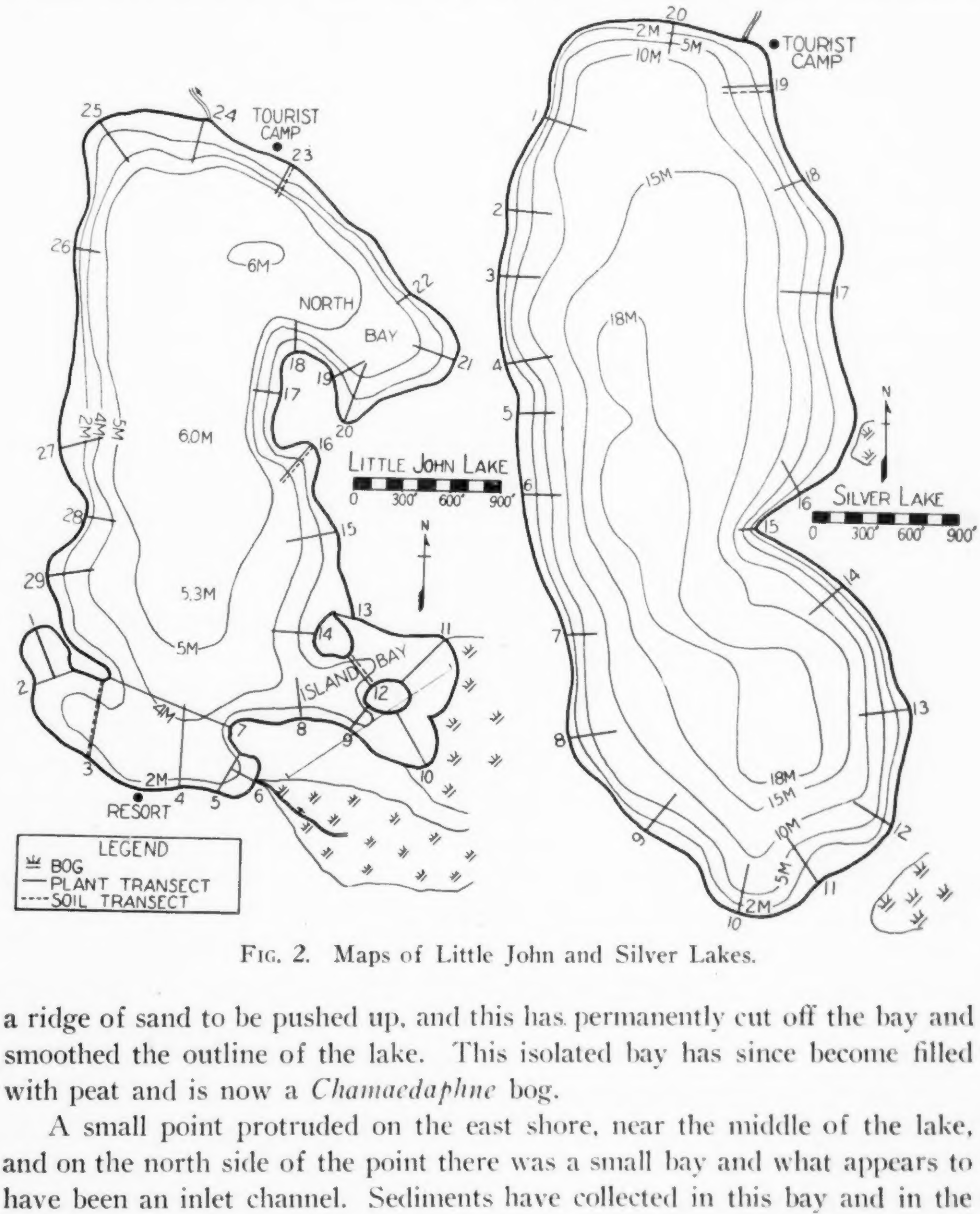

FIG. 2. Maps of Little John and Silver Lakes.

a ridge of sand to be pushed up, and this has permanently cut off the bay and smoothed the outline of the lake. This isolated bay has since become filled with peat and is now a *Chamaedaphne* bog.

A small point protruded on the east shore, near the middle of the lake, and on the north side of the point there was a small bay and what appears to have been an inlet channel. Sediments have collected in this bay and in the shallow water near the point. Ice activity pushed up ridges of sand and gravel, filled the bay and extended the point until at present it is more than 15 meters

longer than it was originally. There is evidence, by the presence of two very marked sandy ramparts, of two major extensions of this point. The development of the point has been such that its width was greater than the distance covered by the advancing ice from both sides of the point and consequently there is a low region between the ramparts that furnishes a habitat for a moist flora. The point has advanced into deep water and off the end there is a marked drop off.

At the northeast end of the lake there is a low portion in the shoreline through which the lake had its outlet. This flowed into Trout Lake. There also occurred considerable sedimentation of sand and gravel. This was pushed up into ridges by the ice and has blocked the outlet. Until the recent drop in lake level, the outlet stream has always been strong enough to erode through any ridge formed by the spring ice push, but at present there is an almost uniform sand and gravel rampart across the outlet and a natural resumption of this channel will be difficult unless there is a considerable increase in lake level.

Silver Lake at present must be classed as a seepage lake, though the outlet was functioning as recent as 1926. Prof. C. Juday observed it in use during 1902 and 1904. The frequency of the drainage when the lake was cutting its lower beach mark cannot be stated, but when the lake was at the level of a strongly developed beach, .7 of a meter above it, the drainage was continuous, and the outlet was probably a meandering stream, several meters wide.

The upper beach mark on the north side of the point is above the barrier which is across the old inlet, and it is certain that at its highest level the lake extended at least a short distance into the bay. At present, the whole inlet channel is filled with bog or swamp and no water appears to be entering the lake at this point.

The soils of the shallow water are either rocky or sandy and those of the deeper water are sandy until one reaches the ten meter depth, and then, in most parts of the lake, organic sediments are abundant. The upland soils have been mapped as Vilas Loam (Whitson and Dunnwald, 1915), and these are the soils that have been reworked by the lake water and quite regularly distributed as described above. In the southern portion of the lake a reddish sand or silt was frequently observed. This appeared to be a ferrous compound that had been deposited in a crust over the yellow sand in shallow water. The origin of this reddish soil seems to be associated with a bottom dwelling algae, but the formation of this material was not investigated.

The water of the lake is clear with little color or turbidity. Its color ranges from 0 to 8 and the conductivity from 59 to 60. The water is neutral to slightly alkaline with a pH of 7.6 to 7.8 and a bound carbon dioxide content ranging from 14.3 to 20.0 parts per million. With these properties, Silver Lake is well within the range of medium hard water lakes given above.

The very simple history of this lake is due largely to its original regular shape, steep embankments, relatively great depth, as compared with its area, and its sandy and rocky soils. For these reasons it has remained comparatively primitive and of the three lakes discussed, the sum total of youthful characters of Silver Lake appear to be greater than in the two others.

THE FLORA AND ITS DISTRIBUTION

Silver Lake contains fourteen species of vascular plants and one species of *Chara* (Table 4). These are species which occur in both the medium hard water lakes and in lakes of softer water. The latter species are less abundant than the former.

TABLE 4. Specific crops and their vertical distribution in Silver Lake

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Chara sp.	.09	35	65	0
Eleocharis acicularis	.23	67	33	0
E. palustris	5.15	100	0	0
Gratiola aurea, f. pusilla	.35	100	0	0
Isoetes macrospora	.62	78	22	2
Juncus pelocarpus, f. *submersus*	.41	97	3	0
Lobelia Dortmanna	.47	100	0	0
Najas flexilis	1.12	31	36	33
Polygonum natans, f. *genuinum*	1.34	100	0	0
Potamogeton amplifolius	.14	43	57	0
P. gramineus, var. *graminifolius*	3.14	59	37	4
P. pusillus	.08	8	16	76
P. Spirillus	.01	50	50	0
Ranunculus reptans, var. *ovalis*	.13	100	0	0
Vallisneria americana	3.79	19	46	35
Total crop	17.07	64	21	15

The total dry weight of plant life in Silver Lake is about 17 kilograms and for a lake of 872,000 square meters, this indicates a surprising sparseness. The total bottom area is only 23 percent colonized and much of this is bare sand. The greatest concentration of plants is in Zone I (0 to 1 meter). Here, 64 percent of the vegetation is found, while in Zone II (1 to 3 meters), 21 percent occurs and in Zone III (3 to 8 meters), 15 percent is present. In Zone I the greatest abundance of individuals is just below the line of wave action, which in most parts of the lake is seldom more than one-half meter below the surface. At this point there appears to be a deposition of organic debris and coarse silts that are washed from the sands of the shore and banks. In these sediments, the plants are comparatively more crowded than elsewhere in a vertical section.

Rickett (1922, 1924), divided the plant profile into three zones similar to that above, and though such a zonation is purely arbitrary it has a com-

parative value and in many cases covers the extreme ranges of natural units of the hydrophytic vegetation. For these reasons the system used by Rickett has been adopted.

The greatest depth at which plants were observed growing in Silver Lake was 6 meters. This occurred at Station 10, and the plants were *Potamogeton pusillus*. They were dwarfed and very slender, which would indicate that they were growing at their maximum depth. According to light transmission studies made on this lake (Table 6), only 6.8 percent of the total sunlight reaches 6 meters at a zenith sun, and the average amount is naturally much less.

Another instance where light penetration appears to be one of the main factors of plant distribution was found at Station 11. Here the water area is somewhat sheltered from the general wave disturbance of the lake and as a result a deposition of the finer silt and sand has taken place at a shallower depth than usual in Silver Lake. This type of sedimentation occurs as shallow as one meter and at this depth 62% of the total sunlight is present. Here the vegetation is massive and the dominant species is *Potamogeton amplifolius*. The vertical range of this species was found to be limited to the silted area between 1 and 1.75 meters. At the maximum depth the light intensity is slightly more than 40% of the total at zenith sun. A superficial analysis of the soils at other places in the lake show that the type noted at Station 11 frequently occurs in six or eight meters of water, but the light penetrating to this depth is less than seven percent.

On the north and west sides of Silver Lake the embankments are steep and are composed of a very rocky glacial drift. Generally the soils of shallow water are composed of rocks and gravel with occasional small pockets of sand. The rocks and gravel have accumulated near the shore and have formed a shelf. The plant life upon this shelf is sparse and composed largely of the bushy form of *Najas flexilis, P. Spirillus, Isoetes macrospora,* and *Chara* sp. The shelf seldom extends into water deeper than one meter and there a slight drop-off, sandy soils predominate. Here plants of *Vallisneria americana,* and *P. gramineus,* var. *graminifolius* occur in addition to those listed above. *Najas* attains more flexuous proportions in deeper water and is the most generally distributed species of plant in the lake. *Vallisneria* flowers abundantly in Silver Lake below the rocky shelf to a depth slightly more than two meters, and *P. gramineus,* var. *graminifolius* has been observed to produce fruit in water nearly three meters deep. Beyond three meters the plants of this species produce only under water leaves, and at its maximum depth of four meters, the plants are seldom more than a few centimeters in height. At four and one-half meters *Vallisneria* and *Najas* reach their maximum depths and these species form the sparse outer fringe of vegetation in the lake except at Station 10 where *P. pusillus* was present.

On the east and southeast sides of the lake there is usually a littoral or

beach flora present and this is also often the important vegetation of the first zone. The beach vegetation is developed best where the soils are sandy and free of rocks. Such conditions are most frequent on the east and southeastern shores of the lake. This is true because the shoreline is slightly more irregular, the water is shallower at a greater distance from the shore, and the banks for the most part are less steep than those of the west shore. Another factor causing the sedimentation of sand on the eastern shores may be the prevailing northwestern wind.

Eleocharis palustris is the most conspicuous plant upon the beach and it extends into .75 meters of water. This forms intermittent but often dense phalanxes over the wet sandy beach and into the water such as illustrated in Fig. 4 for Muskellunge Lake.

The same species, that are found beyond the rocky shelf described above, occur here in shallow water, growing between the rootstocks of *Eleocharis*. Where there is a mixture of gravel and sand on the beach *Eleocharis* is not abundant. Often it is absent and above the water line replaced by several species of *Carex* and *Juncus*, while below, the same species already listed remain. This species may also be associated with *Eleocharis acicularis*, *Equisetum limosum*, *Polygonum natans*, and *Typha latifolia* where the soils show a neutral or alkaline reaction.

The sandy soils in Silver Lake that are neutral or alkaline are usually found in water that is more than one-half meter deep or they are soils that are being continuously deposited by shore currents. Where the sandy soils are somewhat more fixed, such as they are at Station 16, they tend to become acid near the surface. An examination of the soils at Station 16 showed that those upon the beach were slightly acid at the surface, but one-half meter below they were decidedly neutral or alkaline. Soil or water samples from below the surface showed a higher pH and bound carbon-dioxide content than at the surface. The color of the surface sand is yellow to nearly white, but as one digs below it becomes a coffee brown in color, indicating an enrichment from the soil above. This same profile was found in shallow water and there appears to be a degradation of these lake soils such as is described by Wilde (1933) for those of forest and swampland. If the above condition of the soils may be taken to indicate a downward movement of water it might be suggested that the lake basin is a "perched water table", a feature supposedly not uncommon in glaciated regions, especially where the drift is of a sandy nature. The relationship of perched water tables (impervious saucer-like basins in or upon porous soils) to swamps has long been known, but whether this same feature may be found in a lake basin the size of Silver Lake is not known to the writer.

The same soil condition appears to be present where sediments are being deposited but the color of the soils is much more uniform throughout the profile. This may mean that degradation or leaching is going on here as well

as where the soils are somewhat more fixed, but here the upper soils are continuously being renewed by the action of shore currents. These latter soils are, for the present at least, designated as unleached, and those which show an acid nature and lighter color are designated as leached. Below, in the summary of plant communities in Silver Lake, are listed the plants which occur upon the unleached soils in the three zones. The leached sandy soil in Zone I is a phase developed from the unleached, and upon this former there gradually appears a distinct flora which in part seems to be a littoral derivative. This community is particularly well developed at Station 16 but rare at other places in Silver Lake. The relationships of these communities are indicated in the summary by connecting lines and they briefly indicate the trends and stages of aquatic plant succession. It will be noted, especially on comparison with the summary schemes of Muskellunge Lake and Little John Lake, that only a simple and comparatively young stage of ecological succession has been reached in Silver Lake. This is well in keeping with the simple geological history and primitive character of the lake.

SUMMARY OF PLANT COMMUNITIES IN SILVER LAKE

PRIMITIVE LAKE

ZONE I	ZONE II	ZONE III
rocks and sand (unleached)	sand, silt (unleached)	sand, silt (unleached)
Chara sp.	*Chara*	*Najas* (flexuous form)
Eleocharis acicularis	*E. acicularis*	*P. gramineus*, var. *graminifolius*
E. palustris	*Isoetes*	*P. pusillus*
Equisetum limosum	*Najas* (bushy and intermediate form)	*Vallisneria*
Isoetes macrospora	*P. amplifolius*	
Najas flexilis (bushy form)	*P. gramineus*, var. *graminifolius*	
Polygonum natans	*P. pusillus*	
Potamogeton amplifolius	*P. Spirillus*	
P. gramineus, var. *graminifolius*	*Vallisneria*	
P. Spirillus		
Typha latifolia		
Vallisneria americana		

sand (leached)
E. acicularis
Gratiola aurea, f. *pusilla*
Isoetes
Lobelia Dortmanna
Ranunculus reptans, f. *ovalis*

During the three years (1932, 1933, and 1934) that observations were made upon Silver Lake there was a continual fall in the water level. This drop of water level was accompanied by distinct shoreline changes. The soils were redistributed and sand replaced gravel in many places. The vegetation

of the shore and shallow water likewise changed its aspect during the three years. The vegetation in Zone I, at Station 16, became poorer in plants of those species commonly associated with the leached soils. Near the outer fringe of these species, plants of *Najas, P. gramineus,* var. *graminifolius* and *Vallisneria* became more abundant and the soils appeared to be taking on more color. The observations on pH, however, showed little or no change in acidity for identically located soils during 1933 and 1934 but the soils of equal depths during those years were slightly more neutral in the autumn of 1934 than the previous year. This may also be partly due to the fall in water level and the consequent slight change in sedimentation. The significant principle illustrated here is that the plant succession had apparently reversed itself, at least, during the period when the lake level was dropping.

At Station 13 a small colony of *Typha latifolia* was observed in 1932. It contained six poorly developed and badly torn plants. This colony was restricted from spreading upon the shore away from the lake because of the dryness of the sand and the narrow beach, and mechanical activity of the waves prevented a lateral or lakeward extension of the colony. The occurrence of this species in such an unfavorable habitat appeared peculiar, especially because *Typha* is a comparatively rare plant in southern Vilas County and it occurs no place else on the lake or in the immediate vicinity. It did not appear to be a recent introduction for the plants all had very old rootstocks. It is probable that this colony was more extensive earlier in the history of the lake but due to the smoothing of the shoreline with the result that less and less protection from the waves was afforded the species, it neared extinction. This is further suggested by the fact that in this region *Typha* is associated with only the youngest of the seepage lakes or with permanent drainage lakes. During the fall of the water level this colony could spread lakeward and in three years the number of plants has increased from six to eighty-nine (Fig. 3).

In 1932, near Station 19, a small sand spit was forming off an irregularity of the shore. *Eleocharis palustris* became established upon this and bound the sand slightly. It extended over the edge of the spit and further protected it from wave destruction. As the sedimentation of sand was continued the spit was extended across the indentation of the shoreline and formed a bar. *Eleocharis* invaded this newly formed sand area and gave it further permanence. In back of the bar there remained a small lagoon in which *P. Spirillus* and *P. gramineus,* var. *graminifolius* were important species. In 1933 this lagoon did not contain as much water and both species of *Potamogeton* produced plants that were smaller than the previous year. *P. Spirillus* produced only the broad floating leaves. The next year the lagoon contained no water and sedges were rapidly invading the wet sand. Both species of *Potamogeton* were still present. *P. Spirillus* produced again

FIG. 3. *Typha latifolia* growing on sand in Silver Lake. In three years this colony has increased from six to eighty-nine plants. This is probably due to the fall in lake level and greater exposure of sandy beach.

FIG. 4. North end of Muskellunge Lake near Station 52 showing the relationship between *Eleocharis palustris* and the sedimentation of sand.

only the broad leaves, but they were thicker. *P. gramineus*, var. *graminifolius* had lost its characteristic linear lanceolate aquatic leaves and produced instead a few broad and rather leathery leaves which appeared to be well adapted to aerial conditions.

MUSKELLUNGE LAKE

Sections 15, 16, 22, 24, and 25, Township 41 North, Range 7 East

The basin in which Muskellunge Lake is located is roughly crescent-shaped. It was formed by several very large somewhat segmented masses of ice that melted in close proximity of one another. The area covered by this

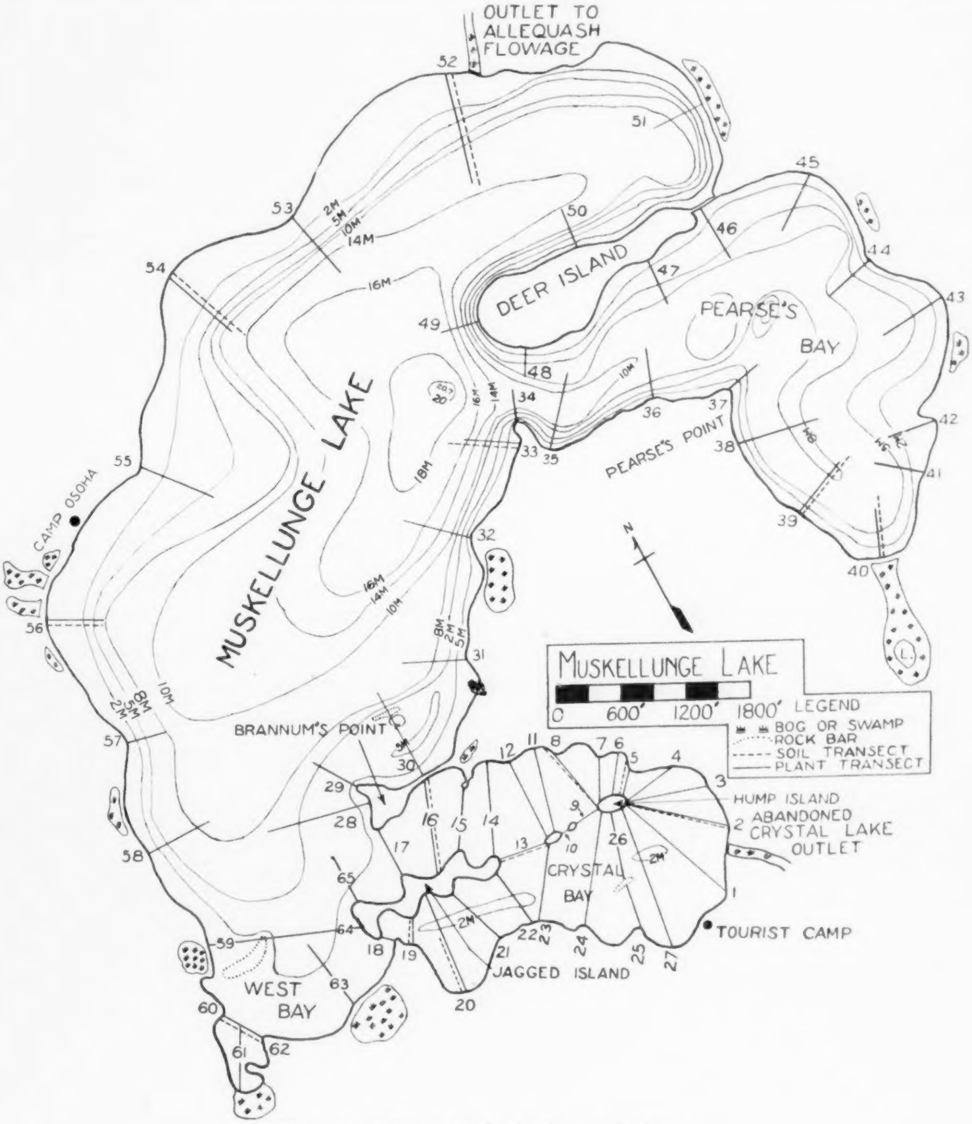

FIG. 5. Map of Muskellunge Lake

lake is 3,723,400 square meters and it has a maximum depth of 21 meters near the center of the lake between Stations 33 and 53 (Fig. 5).

In general the shoreline and the surrounding topography is high and morainic in appearance. There are also low places in the shore line that are now largely occupied by bog or swampland. From the melting ice

masses it is probable that there was considerable outwash. This seems to be a reasonable explanation for the flat areas of sand plain immediately to the south of the lake and on the southern part of the upland between the two ends of the crescent. Crystal and Weber Lakes (Fig. 1) are surrounded by clear crossbedded sand and these may owe their origin partly to outwash from ice in the Muskellunge Lake bed and region.

There are at the present time five islands which vary greatly in size. These occur in Crystal Bay and four of them form nearly a straight line from east to west across the bay. The fifth was a rocky reef, and appeared above the water in the summer of 1934 when the water level dropped .96 of a meter. This likewise has its long axis pointing east and west. The islands probably formed from materials that accumulated in glacial crevasses.

Other islands existed, but have either become joined to the mainland or to another island, or have been eroded to a level below the lake surface. Examples of the first type are Deer Island, and Brannum's Point; of the second, the west segment of Jagged Island; and of the third, the rocky reef through which the transect of Station 30 passes.

The original shape and area of Muskellunge Lake has been altered considerably since its formation. The tendency of the development has been towards a smoothing of the lake outline. This has been accomplished at numerous places, which is indicated in Fig. 5 as bog areas adjacent to the lake shore. The usual development at these places seems to have been first a sedimentation of sand at the mouth of each bay, and then this was pushed up into ridges across the openings. The isolation of the small bodies of water was followed by a rapid change in their aspect, and finally these have ended in being covered over by *Chamaedaphne* and other associated bog plants. One of these isolated bodies of water is still to be found at the end of Pearse's Bay. The portion isolated from Muskellunge Lake was more than 200 meters long and one hundred meters wide. There is a small lakelet near the center of the bog that has almost filled the former lake bed. The conditions which caused the isolation of so large a body of water seem to have been due largely to the narrowness of the lake at the place that is now the head of Pearse's Bay. The sediments carried by shore currents would naturally be deposited here and finally when these were near enough to the surface they were pushed up by the spring ice and a large body of water was isolated.

The soils in the shallow water of Muskellunge Lake are roughly of two types and it is possible upon this basis to separate the lake into two divisions. Crystal Bay and West Bay are shallow and the soils there are largely organic and for the most part, well decomposed. The second division constitutes the remaining part of the lake for there the soils are sand and gravel in the shallow water. The reason for this division is the marked difference in the general depth of the lake basin in these parts. Crystal Bay is formed in a comparatively shallow depression and the accumulation of organic sediments

has been rapid. In the open lake the general depth is increased greatly and these same sediments are seldom found in water shallower than five or six meters.

For a number of years Muskellunge Lake has not drained through the outlet at Station 52. This has been due to the progressive fall in the water level of the lakes of the region, and partly due to the formation of a sandy rampart across the mouth of the outlet. This latter is a common feature in northern Wisconsin and it undoubtedly has some importance in the isolation of a lake from its drainage system, and speeding up its future development. At present there is no known influx of water from streams or springs into Muskellunge Lake and consequently it must be considered as a seepage lake.

Early in the history of the lake there was an inlet between the transects of Stations 1 and 2. This stream flowed from Crystal Lake (see Fig. 1) into Muskellunge Lake, but for what length of time cannot be stated. At present there is an old sandy rampart more than 2 meters high across this channel on Crystal Lake, and on the shore of Muskellunge Lake there is also such a rampart though it is not as high. It is certain, from these observations, that the channel has not functioned at least for several centuries.

The fluctuation of the water level in Muskellunge Lake has been considerable since 1929. Measurements made at that time and in August 1934 show that the fall was approximately 1.1 meters. The result has been an exposure of a wide beach varying in width from 12 to 30 feet, and a redistribution of many soils especially those of an organic nature in shallow water. Bogs that formerly extended into the water were left high above, and in several instances the aquatic organic soils in front of the bog formation has been carried away and replaced by sand. Many of the plants in the bogs have died and are being replaced by an upland flora.

The mineral soils are like those of the upland in composition, and are of the Vilas and Plainfield types. These have been reworked into two general profiles illustrated by transects taken through Station 16 and Station 40.

In the first the maximum depth of the water is one meter. Samples of soil were secured from .2, .5, and .7 of a meter depth off the mainland and at the same depths off the north side of Jagged Island, and also half way between these points at one meter. Analysis of those soils near the mainland showed that at .2 of a meter the percentage of volatile matter present was less than 5%, at .5 of a meter, more than 10%, at .7 of a meter, about 25%, and at 1 meter, the percentage was nearly 70%. These same general results were found for the other samples though slightly less at each depth. Observations were made on the pH of the same samples and they were as follows for those near the mainland. At .2 of a meter the pH was 6.3, at .5 of a meter, 6.8, at .7 of a meter, 5.8, and at 1 meter the pH was 5.7. The other series of samples showed approximately the same reactions for identical depths. Samples

were not taken at the shore, because the soil there is composed only of coarse gravel (Fig. 6).

The analysis of the soils at Station 40 showed that there was only .52% volatile matter present at .2 of a meter, 1.77% at 1 meter, 1.29% at 3.5 meters, and 28.34% at 5.5 meters. The pH observations were made from the sandy beach above the wave limit into 8 meters of water. On the beach the pH was 5.0, but at the water line there was a rise to 7.0. Then at .2 of a meter, 5.8 was recorded and this was also found to be present at 1 meter. At 1.5 meters a slight rise was observed; at 2 meters the pH rose to 6.8, but at 4 meters another drop occurred and a pH of 6.0 was observed. At 6 meters the pH dropped still further to 5.8, where it remained constant as far down as observations were made.

Fig. 6. Crystal Bay in Muskellunge Lake from Station 15 showing a rocky spit formed by ice and wave activity. Part of Jagged Island is to be seen in the background.

This type of pH profile was encountered at every station where there were mineral soils present in the shallow water. The rise in pH at 2 meters and drop again at 4 meters at Station 40 was a surprising encounter, but this general curve appears to be the rule rather than the exception in the three lakes discussed. The depth at which the pH rises is very variable and may be determined by the amount of wave activity at each location. The soils of this profile as well as several others were tested with two different types of field pH indicator kits and the soils were also checked with a Quinhydrone apparatus. In all three instances the same curve was observed. A satisfactory explanation for this curve has not been found, but an examination of the soil types has suggested that the sandy soil upon the shore has a low pH because it is leached as already described. The rise in pH at the edge of the water may be due to the effect of phytoplankton that is constantly being washed

upon the shore. The drop in pH at .2 of a meter depth may be likewise due to a form of leaching accomplished by wave activity, and the greater this motion the greater may be the leaching. The point of rise in pH of the sandy soils may represent a depth below which leaching takes place. At this point there might be the beginning of a zone where there is still enough water movement to prohibit the deposition of the organic sediments that form lower down the profile and show an acid reaction. Associated with this pH curve there seems to be a rather definite distribution of plants, but this will be discussed below.

The water of Muskellunge lake is softer than that of Silver or Little John Lakes (Table No. 3). It is on the border line between the soft and medium hard water lakes and floristically it contains elements belonging to extremes of both.

Muskellunge Lake is an example of a lake tending toward the clear, sandy, soft water type in the open lake, while in Crystal Bay the trend is towards soft water and organic soils.

THE FLORA AND ITS DISTRIBUTION

The vascular plants of Muskellunge Lake number thirty species and the important species of algae are three in number (Table No. 5). These latter comprise of species, *Chara, Nitella*, and a species of *Nostoc*.

The dry weight of the total plant crop is about 882 kilograms. This grows on approximately 52% of the lake floor, and represents a much greater percentage of lake area covered by plants than in either of the other two lakes. This is true because Crystal Bay contains extensive crops over nearly its whole area and plants grow to greater depths in Muskellunge Lake than in the two others. Water shallow enough to produce plant life also comprises a greater percentage of the total area of the lake than in the other two described.

TABLE 5. Specific crops and their vertical distribution in Muskellunge Lake

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Bidens Beckii	.76	72	28	0
Castalia odorata	219.91	97	3	0
Chara sp.	6.27	63	27	10
Elatine minima	trace	100	0	0
Eleocharis acicularis	8.18	87	13	0
E. palustris	23.26	100	0	0
Equisetum limosum	.12	100	0	0
Eriocaulon septangulare	148.82	100	0	0
Gratiola aurea, f. *pusilla*	.25	100	0	0
Isoetes macrospora	2.68	95	5	0
Juncus pelocarpus, f. *submersus*	2.30	100	0	0
Littorella americana	1.92	100	0	0

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Lobelia Dortmanna	1.53	100	0	0
Myriophyllum alterniflorum	2.25	89	11	0
M. tenellum	13.29	73	27	0
Najas flexilis	2.95	41	54	5
Nitella sp.	155.20	0	1	99
Nostoc sp.	1.27	0	80	20
Nymphozanthus variegatus	23.01	100	0	0
Polygonum natans, f. *genuinum*	13.80	100	0	0
Potamogeton amplifolius	14.12	18	55	27
P. epihydrus	2.04	86	14	0
P. natans	1.02	100	0	0
P. gramineus, var. *graminifolius*	6.48	63	32	5
P. praelongus	23.16	61	39	0
P. pusillus	.66	0	67	33
P. Robbinsii	146.61	24	48	28
P. Spirillus	.06	50	50	0
Ranunculus reptans, var. *ovalis*	.76	100	0	0
Sagittaria gramineus	.76	100	0	0
Scirpus acutus	52.67	100	0	0
Sparganium angustifolium	3.06	99	1	0
Vallisneria americana	3.61	45	55	0
Total Crop	882.80	75	18	7

The maximum depth at which plants were found growing was seven meters. These were a species of *Nitella* that grows abundantly in Pearse's Bay. At seven meters the percent of the total sunlight at zenith is 4.4 (Table No. 6). The maximum vertical distribution of plants in Silver Lake was found to be six meters and there, 6.8 per cent of the total sunlight occurs. The plants observed at that depth were *P. pusillus*. This species was also found at a similar depth in Muskellunge Lake, and as in Silver Lake, 6.8% of the total sunlight is present at zenith.

TABLE 6. Percent of total sunlight at various depths in three lakes of Vilas County, Wisconsin

Depth (meters)	Silver*	Muskellunge†	Little John‡
1	62.0	62.0	20.0
2	38.0	40.0	12.8
3	26.0	26.0	4.0
4	17.0	16.0	
5	11.0	10.4	
6	6.8	6.8	
7	4.0	4.4	

* Birge and Juday (1932, p. 539).
† Birge and Juday (1932, p. 397).
‡ Birge, E. A. (personal communication).

The flora of Crystal Bay in Muskellunge Lake has been briefly described by Fassett (1930). The following excerpt from his report describes very well the condition in which the writer found this lake in 1932. "Muskellunge Lake, at least at the south end where visited by the writer, has very little shore vegetation. But in the water is a veritable jungle (Fig. 6). The flexuous-stemmed plants listed in table 1 are exceedingly abundant, as are the types with floating leaves listed in table 2. The short stemmed and rosette forms of table 2, while representing several species, are rare and localized." During the summer of 1932 there was noted a slight drop in the water level and there was an increase in the width of the sandy beach and likewise an increase in the rosette forms.

Early in 1933 this lake was studied intensely and the jungle-like vegetation noted by Fassett was found to be the most important element of Crystal Bay. The rosette forms, of which *Eriocaulon septangulare, Gratiola aurea,* f. *pusilla, Isoetes macrospora, Juncus pelocarpus,* f. *submersus, Littorella americana, Lobelia Dortmanna,* and *Myriophyllum tenellum* are the important species, were found to be common plants of the bay as well as the flexuous stemmed species. As the summer progressed and the water level dropped these species attained greater prominence in shallow water. These species listed above, with the exception of *Isoetes,* began to produce flowers as the water receded. The flowering of *Littorella americana* is considered to be a rare occurrence, and though this took place only at the water's edge upon the two smallest islands of Crystal Bay the abundance of the flowers made the narrow fringe purplish in color. In spite of the abundance of flowers and careful check that was kept upon them there apparently were no seeds produced. In 1934 this colony was entirely destroyed by the drought that lowered the lake level.

The species which constitute the jungle-like vegetation are *Bidens Beckii, Castalia odorata, Myriophyllum alterniflorum, Najas flexilis, Nymphozanthus variegatus, Polygonum natans,* f. *genuinum, Potamogeton amplifolius, P. epihydrus, P. natans, P. gramineus,* var. *graminifolius, P. praelongus, P. pusillus, P. Robbinsii, Scirpus acutus, Sparganium angustifolium,* and *Vallisneria americana.* This vegetation which in 1932 and 1933 covered much of the bay except in the channels between the islands, was reduced to about one-tenth of its former quantity in 1934. This was due to the drop in the water level of the lake and the redistribution of the organic soils. These completely smothered great areas of vegetation.

The small bay at the southwest end of the lake contains organic soils that are not as well decomposed as those in Crystal Bay. They contain much plant fibre and represent a type of raw peat. There the vegetation is more restricted in the number of species and the floating leaf type is the most abundant. The soils all show an acid reaction and the vegetation is also mostly of that type. The species typical of this habitat are *Castalia, Nym-*

SUMMARY OF PLANT COMMUNITIES IN MUSKELLUNGE LAKE

PRIMITIVE LAKE

ZONE I

rocks, sand, silt
(unleached)

Bidens Beckii
Castalia odorata
Chara sp.
Eleocharis acicularis
E. palustris
Equisetum limosum
Isoetes macrospora
Myriophyllum alterniflorum
M. tenellum
Najas flexilis (bushy form)
Nymphozanthus variegatus
Polygonum natans, f. *genuinum*
Potamogeton gramineus, var. *graminifolius*
P. natans
P. Spirillus
Sagittaria gramineus
Scirpus acutus
Vallisneria americana

sand, silt
(leached)

Castalia
Elatine minima
Eleocharis acicularis
Eriocaulon septangulare
Gratiola aurea, f. *pusilla*
Isoetes
Juncus pelocarpus, f. *submersus*
Littorella americana
Lobelia Dortmanna
Myriophyllum tenellum
Ranunculus reptans, var. *ovalis*
Sparganium angustifolium

organic soil
(partly decomposed)

Castalia
Elatine
Eleocharis acicularis
Eriocaulon
Gratiola
Isoetes
Juncus
Littorella
Lobelia
Nymphozanthus
P. natans
Sparganium

organic soil
(fiberous, "raw")

Castalia
Eriocaulon
Nymphozanthus
P. natans
Sparganium

Swamp and bog

ZONE II

rocks, sand, silt
(unleached)

Bidens
Chara sp.
Isoetes
Myriophyllum alterniflorum
M. tenellum
Najas (intermediate form)
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. epihydrus
P. gramineus, var. *graminifolius*
P. praelongus
P. pusillus
P. Robbinsii
P. Spirillus
Vallisneria

organic soil
(well decomposed)

Bidens
Castalia
Chara sp.
Elatine
Eleocharis acicularis
Isoetes
Myriophyllum alterniflorum
Najas
Nitella sp.
Nostoc sp.
Nymphozanthus
Polygonum
Potamogeton amplifolius
P. epihydrus
P. gramineus, var. *graminifolius*
P. praelongus
P. pusillus
P. Robbinsii
Vallisneria

ZONE III

sand, silt
(unleached)

Chara
Najas (flexuous form)
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. gramineus, var. *graminifolius*
P. pusillus
P. Robbinsii

organic soil
(well decomposed)

Najas
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. pusillus
P. Robbinsii

phozanthus, P. natans, and *Sparganium.* In the open lake the vegetation belongs to the early phases of aquatic plant succession and indicates that Muskellunge Lake is a comparatively young body of water in this portion of its area. The dominant species of shallow water are *Isoetes, Myriophyllum tenellum, Najas, P. gramineus,* var. *graminifolius,* and *Vallisneria.* These are usually more abundant near the outer edge of the first zone. In deeper water, usually in Zone III, there is a change of the soils from sand to the well decomposed organic type. Upon these, *P. amplifolius, P. pusillus, P. Robbinsii,* and *Nitella* are often very abundant and form the outer fringe of the vegetation. The outermost member is usually *P. pusillus* or *Nitella* sp.

Pearse's Bay contains a vegetation that is quite different from the remainder of the lake in its abundance of deep water species. The most abundant form is *Nitella* and this occurs in enormous masses over the floor from about three meters to a depth of seven meters. *Potamogeton amplifolius* and *P. Robbinsii* are important species on organic soils to a depth of five meters. In this bay there was locally an abundance of *Nostoc,* a massive alga, that was often brought up to the surface in large quantities in the dredge.

In the shallow water at Station 40, the plants most frequently associated with sandy, acid soils were noted as occurring in the area of low pH described above, and those most commonly found upon the more alkaline soils occurred near the two meters depth where the soils showed a higher pH. How significant these observations are is not known at present, but there appears to be a definite relationship.

LITTLE JOHN LAKE

Sections 20 and 29, Township 41 North, Range 7 East

Little John Lake is a comparatively small body of water with 672,000 square meters of surface, a maximum depth of six meters, and an abundance of dissolved mineral salts in the water (Table No. 3). It has the hardest water of the three lakes discussed here, and it is a type of lake that is not very abundant in the region. The striking feature of this lake is its turbidity, which is due largely to the presence of great quantities of phytoplancton. These algae are abundant throughout most of the season of open water and give to the water a greenish yellow color during most of this time. Another feature of this type of lake is the abundance of well decomposed organic sediments in shallow water. These almost mask the mineral soils except where wave action is strongest. This type of lake has, as a rule, a steady influx of water, but during 1934 Little John Lake had much less than usual.

The topography in which Little John Lake is located is rough and morainic, except at the southern end, where there is a suggestion of local outwash plain. The basin of this lake has also resulted from the melting of an ice mass. The irregularity of the outline suggests that the mass of ice

was heavily loaded with glacial debris, and this is further emphasized by the fact that the lake is shallow with some irregularity upon its floor. This irregularity is most apparent at the southern end of the lake, but does not appear very plainly upon the map, for these features are intermediate between the contours.

The soils of the upland surrounding the lake on the west, north, and east are Vilas, Loamy Sand, and on the south the soil is Plainfield, Fine Sand. Much of the Vilas soil contains rocks and small boulders, and this, with the finer particles, makes up the mineral soil of the lake.

Along most of the shoreline except during high water, there is a narrow beach, which is rocky where the embankments contain the drift described above (Figure 7). At the north end of the lake extending from the transect of Station 25 (Fig. 2) to nearly that of Station 23, the history has been slightly different from the greater part of the open lake and here there is a well developed sandy beach during low water. At the head of each bay the shoreline is boggy where the plant life is encroaching upon the lake.

Two small islands are found in the southeastern part of the lake, where their presence has materially affected the sedimentation and plant life of Island Bay. Their origin is the morainic materials associated with ice as above described.

The original outline of the lake has been modified at the southeast, southwest, and northwest ends of the lake more than elsewhere. Near Station 6 there is an ice push across an inlet, but the scanty inflow of water is not prohibited, for it has eroded channels through the barrier. A large swamp extends up the valley along the stream course. This may have been partially filled with water, and possibly a part of the lake in its early history. At the head of Island Bay a swamp has formed and covers a considerable area that was formely the lake bed.

On the southwest side of the lake a point extends from the mainland more than one hundred meters. It is rocky and the construction shows that it was partly, if not wholly, built by ice pushing up ridges of sand, gravel, and rocks from the shallow water. These ridges are very marked near the end of this point.

The point on the eastern shore opposite, was not formed in the same manner, but is considerably higher and composed of rocky drift that has not been reworked by the lake waters.

At the northwest end of the lake, approximately the distance from the transect of Station 25 to a place half way between the transects of Stations 23 and 24, is a series of ice pushes, which form the shore embankment. This series has cut off a large portion of the early lake, and this was developed into a swamp land which contained, until recently a heavy growth of timber. Through the rampart the outlet has continued to flow, though this is usually

only during early spring and summer. When the lake was first studied the outlet was partially blocked by an old beaver dam, but recently this was torn out and a channel was dug through the debris. No effect on the late summer drainage has been accomplished.

In recent years there seems to have been very little ice activity in the lake, but in the past there must have been a great deal. This is suggested at Station 26 by old soil ramparts that were eleven feet above the lake level of 1934.

TABLE 7. Percentage of volatile matter in soils of Little John Lake

Depth in meters	*Stations* 3	16	23
0.5	——	2.31	.85
1.0	——	3.08	——
1.5	2.45	3.10	——
2.0	3.10	3.13	1.31
2.5	70.26	33.86	——
3.0			1.20
5.0			1.25

FIG. 7. The northwest end of Little John Lake from Station 27 showing the high banks which surround the greater part of the lake and the gravel and small stones that have been washed from the embankments.

The open part of the lake, because of its greater expanse and water movement, has remained more primitive than the bays. Sedimentation has been less rapid. The soils at Station 23 are quite typical of the open lake on a smooth shoreline and the percentage of volatile matter found in these is shown in Table No. 7. The volatile matter in the soils of Little John Lake appears to be largely of an organic nature, and their abundance might be taken to represent the speed of sedimentation. The remainder of these soils is silt, sand, and gravel, of which the most abundant mineral is quartz.

At Station 16 the effect of an undulating shoreline upon sedimentation of organic soil is well marked. Between 2 and 2.5 meters the change in the volatile materials is more than 30%, and physically the soil at 2.5 meters resembles that of the deep water.

In the bays except on exposed parts of the shoreline the soils are all of the organic type and are represented by Station 3 in the above table. The great abundance of volatile material at 2.5 meters is probably caused in part by the abundance of partly decomposed tissues of *Najas, Potamogeton,* and *Anacharis.* At Station 3 pH observations on the soils were made from the point toward the mainland and showed the following range: shore, pH 6.8; .2 meters, pH 6.0; .7 meters, 6.0; 1.5 meters, pH 5.3; 1.7 meters, pH 6.8; 2 meters, pH 5.9; 2.5 meters, pH 5.7.

The water of Little John Lake is higher than that of Silver or Muskellunge Lakes in its color, pH, and conductivity (Table No. 3), but the bound carbon dioxide content is slightly less than that of Silver Lake.

The water level of this lake has remained more constant than in the other two, but in 1934 there was a drop of .3 of a meter. This exposed much more sand and as the waves beat upon the shore they removed the finer sediments that had previously accumulated in shallow water. The lake became more youthful in the appearance of its shoreline.

The Flora and its Distribution

Little John Lake contains twelve species of vascular plants and a species of *Chara* (Table No. 8). They are forms found associated with the hardest waters of Wisconsin lakes and there are also a few forms that are abundant in the softest waters. These latter, however, constitute a minor part of the flora. The total area of the lake floor that is colonized by plants is but 31% of the whole, or 213,505 square meters.

The vegetation is largely concentrated into Zone I, and unlike the other lakes, there is a total absence of the larger aquatic plant life in Zone III.

Table 8. Specific crops and their vertical distribution in Little John Lake

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)
Anacharis	2.52	0	100
Chara sp.	.61	88	12
Eleocharis acicularis	trace	100	0
E. palustris	4.31	100	0
Isoetes macrospora	trace	100	0
Myriophyllum tenellum	trace	100	0
Najas flexilis	78.03	61	39
Nymphozanthus variegatus	11.30	100	0
Potamogeton amplifolius	.20	100	0
P. gramineus, var. *graminifolius*	.04	100	0
P. pusillus	2.08	36	64

P. Richardsonii	12.56	83	17
Sparganium angustifolium	trace	100	0
Total crop	111.65	82	18

The total dry weight of the plant crop in Little John Lake is slightly more than 111 kilograms. The area covered by plants in this lake is almost the same as that covered by them in Silver Lake, yet the crop is nearly seven times as great. The average crop per square meter is .52 grams as compared with .08 of Silver Lake (Table No. 9).

The vegetation of the open lake may first be considered for it more nearly represents the early type of vegetation in Little John Lake. Here the most general and abundant species is *Najas flexilis.* It occurs in water that is from .2 to 3 meters deep growing on the sandy and rocky soils of shallow water and on the organic soil of deeper water. There is a general increase in abundance of this species as the soils become more organic and the water deepens to 1.5 meters. This seems to be due to the combined change in the soils and the lesser activity of the water at greater depths. *Najas flexilis* and *Potamogeton pussillus* grow to a depth of three meters. This is the maximum depth at which vegetation was observed. The reason for such a shallow colonization could not be determined, though several factors which might limit the downward distribution of plants are very pronounced in the lake. One factor, the turbidity of the water, may limit the amount of light which reaches below 3 meters to such an extent that plants cannot grow. Light measurements made by Dr. E. A. Birge (Table No. 6) on Little John Lake show that only 4% of the total sunlight reaches 3 meters at zenith. Readings with a six inch white disc were made on Little John Lake in August 1933 and give an indication of comparative transparency with that of Silver and Muskellunge Lakes. This disc was visible only to a depth of 2.2 meters in Little John Lake and in Silver Lake it is visible to a depth of 8.1 meters and to 5.2 meters in Muskellunge Lake. Another factor, that of rapid sedimentation of organic materials occurs below 3 meters in many parts of the open lake. At the lowest depths of plant colonization specimens were frequently found covered with a muddy deposit and they were apparently dying.

Other species occurring in the open lake and North Bay are *Potamogeton amplifolius, P. gramineus,* var. *graminifolius, P. pusillus, Sparganium angustifolium, Nymphozanthus variegatus,* and *Chara* sp.

Potamogeton amplifolius was found growing in abundance only at Station 20, in North Bay. The conditions there are not like those in the other bays, but resemble, with the exception of the shallow water (0 to 1 meter), the conditions of the open lake. *P. gramineus,* var. *graminifolius* was found only at Station 7 growing in sandy soil, while *P. Richardsonii,* and *P. pusillus* were generally distributed. *Sparganium angustifolium* and *Nymphozanthus variegatus* are not abundant in the open lake and grow only along the protected

shore of Stations 18 and 19. There, considerable organic soil has accumulated and this seems to be the reason for the appearance of these species.

Chara was found in considerable abundance at Stations 7 and 24, but was sparse at other places except in the bay at Station 3.

The bays are remarkably filled with vegetation, especially the small bay at the southwest end of the lake and the east end of Island Bay. Much difficulty was experienced in propelling a boat through the vegetation in these two bays and painted terrapins surprised while basking in the sun were often unable to escape through the floating mat. The beavers, which have a large house between the transects of Stations 9 and 10 have cleared runways through the tangle and these seem to be utilized by many other animals including terrapins and small fish. The plant that makes up almost the total crop in Island Bay is *Najas flexilis*. This species also makes up about four-fifths of the vegetation in the southwest bay. The ecological form of this species in the bays is the long lax type while in the open lake this form as well as the short bushy type is present.

The most primitive floristic condition of Little John Lake undoubtedly exists in the open lake where the shallow water soils are still sandy or only slightly covered by organic materials. Upon such soils plants of *Chara* sp., *Isoetes macrospora*, *Myriophyllum tenellum*, *Najas flexilis*, and *Potamogeton gramineus*, var. *graminifolius* grow. The first species is bushy or tree-like under such conditions as noted above. Chara is only sparsely present as is also *P. gramineus*, var. *graminifolius*. The lesser abundance of this last species in Little John Lake as compared with Silver and Muskellunge Lakes seems to be due to the greater abundance of organic soils in Little John Lake. If this is the reason for the comparatively lesser quantity then it seems reasonable to consider *P. gramineus*, var. *graminifolius* as colonizer of primitive soils and its little abundance an indicator of lake maturity. Wherever the water of the open lake is deep enough to allow the sedimentation of silt particles and some organic soils and not beyond the depth of other growing factors, *Potamogeton Richardsonii*, *P. amplifolius*, and *P. pusillus* may become abundant as in North Bay. When this habitat develops, *P. gramineus*, var. *graminifolius* disappears.

In 1932 *Isoetes macrospora* was collected only off the end of the point near the southwest end of the lake. Here it grew in water no deeper than in .2 of a meter. The soils were sandy and had a pH of 6.0. Two years later it was found to be slightly more abundant in the shallow water of Station 25. It was associated with *Eleocharis acicularis* and *Myriophyllum tenellum*, which are also members of the "rosette flora," characteristic of the soft water sandy lakes described by Fassett (1930). The occurrence of the last species was especially a surprise, for it is one of the most important members of the "rosette flora," and was considered to be a derivative of the beach zone. Instead it now appears, from the observations in this lake and several others,

to be a species similar in behavior to *P. gramineus*, var. *graminifolius*. However, it remains a member of a lake flora longer than the latter where a lake develops towards the soft, sandy, clear water type, or disappears earlier if the lake retains its hardness of water and develops into the type of lake which has an abundance of colloidal organic soil.

SUMMARY OF PLANT COMMUNITIES IN LITTLE JOHN LAKE

PRIMITIVE LAKE

ZONE I	ZONE II	ZONE III
rocks, sand, silt (unleached)	silt, organic soil (Unleached or well decomposed)	Organic soil (well decomposed)
Anacharis canadensis	*Anacharis*	No plants
Chara sp.	*Chara* sp.	
Eleocharis acicularis	*Najas* (slender form)	
E. palustris	*P. pusillus*	
Isoetes macrospora	*P. Richardsonii*	
Myriophyllum tenellum		
Najas flexilis (bushy form)		
Nymphozanthus varigatus		
Potamogeton gramineus, var. *graminifolius*		
P. Richardsonii		

silt, organic soil
(well decomposed)

Anacharis
Chara
Najas (slender form)
Nymphozanthus
P. amplifolius
P. pusillus
P. Richardsonii

organic soil
(not well decomposed)

Sparganium augustifolium
Nymphozanthus

Swamp and bog

The two southernmost bays and Island Bay present examples of rapid sedimentation and its effect upon the vegetation. The areas of these bays are small enough to be almost always free from rough water and consequently the sedimentation is rapid. There seems to be three sources of these sediments, (1) from the decay of an abundant vegetation in the bays (2) from organic materials blown into the lake, and (3) from sediments from the main part of the lake carried by shore currents and dropped in the still water of the bays.

At the head of each one of the bays small *Chamaedaphne* bogs are developing. These are encroaching slowly upon the water in back of a narrow zone of *Carex*. Out in front of these bogs there seems to be a more rapid sedimentation in process. The particles which make up the sediments are larger than those of deeper water and contain more fiber. These are apparently the transition sediments into what is commonly known as raw peat. The plants inhabiting these soils are *Sparganium angustifolium* and *Nymphozanthus variegatus*. They represent species that belong to the end of the aquatic plant succession series in Little John Lake. The following scheme summarizes the plant communities in Little John Lake and indicates their relationships.

A COMPARISON OF THE MEDIUM HARD WATER LAKES OF SOUTHERN VILAS COUNTY, WITH TWO HARD WATER LAKES OF SOUTHERN WISCONSIN

To compare those lakes of southern Vilas County that are described above, with the two hard water lakes of southern Wisconsin, that have been studied in the same manner, a brief discussion of the regions and their dissimilarities is necessary. A fundamental difference in the two regions is at once apparent in the bed rock of each. Whether this is the prime difference and the factor which governs the many other features, cannot be definitely stated. However, the granite and gneiss rocks of Vilas County are covered with a mantel of sand and other soils relatively poor in plant nutrients, while the localities in which Green Lake, and Lake Mendota are present the bed rock is limestone and the soils are relatively rich in the available bases so important to the growth of most plant life.

Both regions are located within the area of Wisconsin drift, but the nature of this drift differs in various parts of the state. That of southern Vilas County is essentially sand and gravel, and in the part of southern Wisconsin under discussion the drift is essentially clay, silt, and gravel. In short, one is a region of acid soils, and the other a region of alkaline soils. The glaciation of northern Wisconsin is more recent than in southern Wisconsin and the natural perfection of the drainage is completed to a much lesser degree.

As stated before, the lakes of southern Vilas County are developed in depressions left by the melting of the last ice sheet, but in contrast to these, the two southern lakes occupy depressions in limestone bed rock. The derivation of dissolved minerals in the waters of the southern lakes is from the sediments of streams flowing over the limestone drift and from the mechanical and chemical weathering of the rocky lake cliffs. The streams of Vilas County in contrast, flow over an acid drift and carry a comparatively small amount of mineral plant nutrients in their loads. There are no rock

or soil lake cliffs and as stated elsewhere, there is at present no very great influx of water into these lakes.

With such striking regional and physiographic differences as shown by the areas of northern and southern Wisconsin, it is logical to expect that there will be a vast difference in the water mineral content of the two regions. This expectation is confirmed by conductivity measurements upon the waters of these lakes (Table No. 3). The highest reading of conductivity in the three northern lakes under discussion was made in Little John Lake. This reading shows the conductivity to be less than one-fourth as much as is found in Lake Mendota.

The original soils of the three northern lakes are predominantly sand while those of Green Lake and Lake Mendota contain more clay and silt than sand. Those soils that have developed in the bays and below the depths of wave activity in the northern lakes are largely organic and vary from a colloidal, well decomposed type to raw acid peat. In Lake Mendota and Green Lake, these secondary soils are also partly colloidal and peaty, and in addition, large quantities of marl are present. There appears to be a difference between the colloidal soils of the soft and medium hard water lakes and those of the hard water lakes, but what that difference is, has not been determined. There is still much to be learned about aquatic soils.

A study of the lake areas and depths brings out another difference which influences a comparison based on plant abundance (Table No. 3). The smallest of the northern lakes is .67 square kilometers in area and its maximum depth is about 6 meters. The largest northern lake (Muskellunge Lake) is 3.72 square kilometers in area and has a maximum depth of 21 meters. Comparing these figures with Lake Mendota, the larger southern lake, it is evident that the latter is more than ten times larger than the largest of the three northern lakes, while in depth it exceeds Muskellunge Lake by only four meters. Green Lake is a little more than three times the area of Muskellunge Lake, but in maximum depth Green Lake is more than three times deeper than it or Lake Mendota. The relationship between area and depth in a lake as related to plant life is a variable feature and there is no general rule that can be stated. It is however, reasonable to expect a proportionately greater abundance of plant life as the area increases in a lake of irregular outline than in a lake of smooth outline. With the comparative increase of depth in lakes, plant life may become scarcer, if there is as a result, an absence of shelves or bars upon which it can grow. Upon the steeper slopes of the lake bed, fine sediments do not usually become fixed and plant succession is much slower on these areas. The vegetation of the five lakes is similar in the majority of species, but the northern lakes contain a dominant element in their flora that produces less tissue than that in the two southern lakes. This is the second type listed by Fassett in the *growth form* classification already discussed. A small lake, such as Little John or Silver,

that has a limited range of soils will usually contain a limited flora of larger aquatics. These lakes contain twelve and fifteen species respectively. Muskellunge Lake contains a variety of soils and habitat conditions and a flora of thirty-three species. Rickett (1922, 1924) has recorded twenty-one species for Lake Mendota and twenty-seven for Green Lake. In the latter he has listed a number of algae. These also occur in Lake Mendota. A comparison of the algae flora in the two regions has not been made, but it may be generally stated that in the soft and medium hard water lakes of northern Wisconsin, especially those that are clear and have sandy soils, the quantity of attached algae is considerably less than in the two southern Wisconsin lakes. In the lakes of Vilas County *Cladophora* was not encountered, but this alga is an important plant in Lake Mendota and is also present in Green Lake. Only once has the writer seen filamentous algae abundant in the lakes of Vilas County. This was present in the northwest end of Allequash Lake (see general map, Fig. 1) in late August, 1933. The alga, a species of *Spirogyra,* formed mats several inches thick and covered acres of water surface. It was

TABLE 9. A comparison of the colonized area and plant abundance of five Wisconsin lakes

LAKE	*Area Colonized* (hectares)	*Total Crop* (kilograms)	*Average Crop per sq. m.* (grams)
Silver	20	17	.08
Muskellunge	193	882	.45
Little John	21	111	.52
Green	857	1,527,900	178.00
Mendota	1,040	2,100,000	202.00

buoyed up by pockets of gas and was a bright yellow color. The only alga other than *Chara* and *Nitella* that was large and abundant enough to be considered in these studies was a species of *Nostoc* in Pearse's Bay of Muskellunge Lake. This alga was localized to that portion of the lake.

The total crops of the five lakes show a surprising range of productivity. These are compared in Table No. 9 and show their relationship to the area colonized by the plants in the respective lakes, also the average crop per square meter.

The much greater weight of plant life in the two southern lakes stand out as markedly as do the other comparisons already made. The explanation for such great difference of plant weight in the two regions appears to be the following: (1) sandy soils predominate in the north while silt and clay are more abundant in the south, (2) there is greater bulk of tissue in the dominant species of the southern lakes, and (3) there are also greater areas of lake bottom covered by the plants in these lakes. Another factor, that of temperature, may have some effect on the abundance of the crop.

In the northern lakes especially, but also in the southern lakes, it appears as though one might take the conductivity of the lake waters as an indicator

of the abundance of plant crop present in a specific lake. This indicator, however, appears to have limitations where marl is present in great quantities, for often in such lakes there is almost an absence of aquatic vegetation except where inlets enter.

The vertical distribution of plants in the five lakes show great variation in the percentage of the total crops in the three zones (Table No. 10), but the number of factors, which determine this distribution will not permit a general statement with the data now at hand.

TABLE 10. Comparison of total plant abundance in percent of whole crops

LAKE	Zone I (0 to 1m.)	Zone II (1 to 3m.)	Zone III (3 to 8m.)
Silver	64	21	15
Muskellunge	75	48	7
Little John	79	21	0
Mendota*	30	45	25
Green*	9	40	51

The total absence of vegetation in Zone III of Little John Lake has been suggested as due to the rapid sedimentation of organic soils, and the turbidity of the water, which does not permit a sufficient amount of light for the larger aquatic plants in this zone. In contrast to this absence of plant life in Zone III of Little John Lake is the occurrence of 51% of the total crop of vegetation of Green Lake below the three meters depth. The great bulk of this crop according to Rickett (1924) is made up of *Chara*. This plant is commonly found in enormous quantities and would naturally have marked effect on profile studies.

SUMMARY

1. In a series of medium hard and soft water lakes of southern Vilas County, Wisconsin the ecological factors and vegetation have been investigated on a quantitative basis. The results have been divided into two parts, Part I, the medium hard water lakes, and Part II, the soft water lakes.

2. The physiography of southern Vilas County and its history are discussed with reference to its effect upon lake ecology, the vegetation of the region, and the lake development.

3. The medium hard water lakes of the region contain the most complex studies and the three lakes here discussed present a typical cross section of these problems.

4. The abundance of each plant species was determined from dry weight by denuding quadrates located along profiles through natural ecological divisions in the lakes. Soils from each quadrate were correlated with plant crop, slope of the lake basin, and water movement.

5. Soils of a colloidal organic type found in comparatively shallow water in drainage lakes support the greatest abundance of vegetation while sand supports the least.

* From Rickett (1924).

6. The effect of light on plant distribution is apparent, but these records are still too incomplete to draw any conclusions from field observations.

7. A comparison of the plant life is made between two lakes of southern Wisconsin and three of Vilas County. A comparatively scanty crop in the northern lakes is explained by, (1) the dominance of sandy soils in these lakes, (2) the greater bulk of tissue in the dorminant species present in the southern lakes, and (3) greater areas are covered by the plants in two lakes of southern Wisconsin.

8. Marked plant succession in the medium hard water lakes of southern Vilas County takes place only where there is some active hydrographic process at work. Where these processes cause isolation from drainage the trend is toward a soft water plant community, but where the influx of mineral salts is not checked the succession is dependent upon the type of soil which accumulates.

9. The relationship between aquatic plant communities in three lakes has been graphically determined from a study of the specific abundance on various soils, and at various depths in these lakes. The general scheme of aquatic plant succession in southern Vilas County, Wisconsin is being reserved for Part II, after the soft water lakes have been discussed.

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